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Lifespan and reproductive cost explain interspecific variation in the optimal onset of reproduction

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Complete List of Authors:	Mourocq, Emeline; University of Zurich, Anthropological Institute and Museum Bize, Pierre; University of Aberdeen, Institute of Biological and Environmental Sciences Bouwhuis, Sandra; Institute of Avian Research, ; University of Oxford, Edward Grey Institute, Department of Zoology Bradley, Russell; Point Blue Conservation Science, Charmantier, Anne; CNRS, CEFE, UMR 5175 de la Cruz, Carlos; University of Extremadura, Biology & Ethology Research Group Drobniak, Szymon; University of Zurich, Anthropological Institute and Museum Espie, Richard; Technical Resource Branch, Department of Systematic Zoology & Ecology, Behavioral Ecology Group Herenyi, Marton; Eotvos Lorand University, Dept. Syst. Zool. and Ecol.; Szent István University, Department of Zoology and Animal Ecology Hötker, Hermann; Michael-Otto-Institute, NABU Kruger, Oliver; University of Bielefeld, Animal Behaviour; Marzluff, John; University of Washington, College of The Environment, School of Environmental and Forest Sciences Moller, Anders; Université Paris-Sud, Laboratoire d'Ecologie, Systématique & Evolution, CNRS UMR 8079 Nakagawa, Shinichi; University of Otago, Zoology; University of New South Wales, Evolution & Ecology Research Centre, School of Biological, Earth and Environmental Sciences Phillips, Richard; British Antarctic Survey, Natural Environment Research Council Radford, Andrew; University of Bristol, School of Biological Sciences Roulin, Alex; University of Lausane, Ecology and Evolution; T”r”k, J nos; E tv s Lor nd University, Dept. Syst. Zool. and Ecol. Valencia, Juliana; University of Córdoba, Department of Zoology, Cátedra Recursos Cinegéticos van de Pol, Martijn; Netherlands Institute of Ecology, Department of Animal Ecology; Australian National University, Evolution, Ecology & Genetics Warkentin, Ian; Memorial University of Newfoundland, Environmental Science Program Winney, Isabel; University of Sheffield, Department of Animal & Plant

	Sciences Wood, Andrew; British Antarctic Survey, Natural Environment Research Council Griesser, Michael; Univeristy Zurich, Anthropological Institute and Museum

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Full title

Lifespan and reproductive cost explain interspecific variation in the optimal onset of reproduction

Running title

Evolution of delayed onset of reproduction

Authors

Emeline Mourocq,[1*] Pierre Bize,[2] Sandra Bouwhuis,[3,4] Russell Bradley,[5] Anne Charmantier,[6] Carlos de la Cruz,[7] Szymon M. Drobniak,[1] Richard H. M. Espie,[8] Márton Herényi,[9,10] Hermann Hötker,[11] Oliver Krüger,[12] John Marzluff,[13] Anders P. Møller,[14] Shinichi Nakagawa,[15,16] Richard A. Phillips,[17] Andrew N. Radford,[18] Alexandre Roulin,[19] János Török,[9] Juliana Valencia,[20] Martijn van de Pol,[21,22] Ian G. Warkentin,[23] Isabel S. Winney,[24] Andrew G. Wood,[17] Michael Griesser[1]

Author affiliation

[1] *University of Zurich, Anthropological Institute & Museum, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland*

[2] *University of Aberdeen, Institute of Biological & Environmental Sciences, Zoology Building, Tillydrone Avenue, Aberdeen AB24 2TZ, United Kingdom*

[3] *Institute of Avian Research "Vogelwarte Helgoland", An der Vogelwarte 21, D-26386 Wilhelmshaven, Germany*

[4] *University of Oxford, Edward Grey Institute, Department of Zoology, Tinbergen Building, South Parks Road, Oxford, OX1 3PS, United Kingdom*

[5] *Point Blue Conservation Science, 3820 Cypress Drive #11, Petaluma 94954, California, United States of America*

[6] *Centre d'Ecologie Fonctionnelle et Evolutive, CNRS UMR 5175, 1919, route de Mende, F-34293 Montpellier, France*

[7] *University of Extremadura, Biology & Ethology Research Group, Avenida de Elvas, E-06071 Badajoz, Spain*

[8] *Technical Resource Branch, Saskatchewan Environment, 5th Floor, 3211 Albert Street, Regina, Saskatchewan S4S 5W6, Canada*

[9] *Eötvös Loránd University, Department of Systematic Zoology & Ecology, Behavioral Ecology Group, Pázmány Péter sétány 1/c., H-1117 Budapest, Hungary*

[10] *Szent István University, Department of Zoology and Animal Ecology, Páter Károly utca 1., H-2100 Gödöllő, Hungary*

[11] *Michael-Otto-Institute within NABU, Goosstroot 1, D-24861Bergenhusen, Germany*

[12] *Bielefeld University, Department of Animal Behavior, Morgenbreede 45, D-33615 Bielefeld, Germany*

[13] *University of Washington, College of The Environment, School of Environmental and Forest Sciences, 4000 15th Avenue NE, Seattle WA 98195-2100, United States of America*

[14] *Université Paris-Sud, Laboratoire d'Ecologie, Systématique & Evolution, CNRS UMR 8079, 362 Rue du Doyen André Guinier, F-91405 Orsay, France*

[15] *University of Otago, Department of Zoology, 340 Great King Street, PO Box 56, Dunedin 9054, New Zealand*

[16] *Evolution & Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia*

[17] *British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, United Kingdom*

[18] *University of Bristol, School of Biological Sciences, 24 Tyndall Avenue, Bristol BS8 1TH, United Kingdom*

[19] *University of Lausanne, Department of Ecology & Evolution, CH-1015 Lausanne, Switzerland*

[20] *University of Córdoba, Department of Zoology, Cátedra Recursos Cinegéticos, Campus de Rabanales, E-14071 Córdoba, Spain*

[21] *Australian National University, Evolution, Ecology & Genetics, Acton ACT 2601, Australia*

[22] *Netherlands Institute of Ecology (NIOO-KNAW), Department of Animal Ecology, Droevendaalsesteeg 10, NL-6708 PB Wageningen, the Netherlands*

[23] *Memorial University of Newfoundland, Environmental Science Program, Corner Brook, NL A2H 6P9, Canada*

[24] *University of Sheffield, Department of Animal & Plant Sciences, Western Bank, Sheffield S10 2TN, United Kingdom*

e-mail addresses

[1] emeline.mourocq@uzh.ch*; michael.griesser@uzh.ch; szymonmarian.drobniak@uzh.ch

[2] pierre.bize@abdn.ac.uk

[3,4] sandra.bouwhuis@ifv-vogelwarte.de

[5] rbradley@pointblue.org

[6] anne.charmantier@cefe.cnrs.fr

[7] cdlacruz@unex.es

[8] Rick.Espie@gov.sk.ca

[9] yeti01@elte.hu

[9,10] mherenyi@freemail.hu

[11] Hermann.Hoetker@NABU.de

[12] oliver.krueger@uni-bielefeld.de

[13] corvid@uw.edu

[14] anders.moller@u-psud.fr

[15,16] shinichi.nakagawa@otago.ac.nz

[17] raphil@bas.ac.uk; agw@bas.ac.uk

[18] Andy.Radford@bristol.ac.uk

[19] Alexandre.Roulin@unil.ch

[20] juliana@unex.es

[21,22] martijn.vandepol@anu.edu.au

[23] ian.warkentin@grenfell.mun.ca

[24] isabel.winney@gmail.com

Phone numbers

[1] Emeline Mourocq : +34692186305*; Michael Griesser: +41 (0)44 635 54 23 ; Szymon M. Drobniak: +41 (0)44 635 54 34

[2] +44 (0)1224 274145

[3,4] +49 (0)4421 968916

[5] 707-781-2555 ext. 314

[6] +33 (0)4 67 61 32 65

[7] +34-924-289678

[8] 306-787-0024

[9] János Török: +36-1-381-2193; Márton Herényi: n.a.

[10] n.a.

[11] n.a.

[12] +49 521-106-2842

[13] 206-616-6883

[14] +33169155688

[15,16] +64-3-479-5046

[17] Richard A. Phillips: +44 (0)1223 221400; Andrew G. Wood: +44 (0)1223 221400

[18] +44 117 394 1197

[19] +41(0)79 686 08 64

[20] n.a.

[21,22] +61 2 6125 3078

[23] n.a.

[24] n.a.

Corresponding author

*Name: Emeline Mourocq, Address: University of Zürich, Anthropological Institute & Museum, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland,

Telephone number: +34692186305, Email address: emeline.mourocq@uzh.ch

Fitness can be profoundly influenced by the age at first reproduction (AFR), but to date the AFR-fitness relationship only has been investigated intraspecifically. Here we investigated the relationship between AFR and average lifetime reproductive success (LRS) across 34 bird species. We assessed differences in the deviation of the Optimal AFR (i.e., the species-specific AFR associated with the highest LRS) from the age at sexual maturity, considering potential effects of life-history as well as social and ecological factors. Most individuals adopted the species-specific Optimal AFR and both the mean and Optimal AFR of species correlated positively with lifespan. Interspecific deviations of the Optimal AFR were associated with indices reflecting a change in LRS or survival as a function of AFR: a delayed AFR was beneficial in species where early AFR was associated with a decrease in subsequent survival or reproductive output. Overall, our results suggest that a delayed onset of reproduction beyond maturity is an optimal strategy explained by a long lifespan and costs of early reproduction. By providing the first empirical confirmations of key predictions of life-history theory across species, this study contributes to a better understanding of life-history evolution.

KEY WORDS: Age at first reproduction, comparative method, cost of reproduction, family formation theory, life-history theory.

DATA ARCHIVING:

Data are provided in the appendix.

ABBREVIATIONS: AFR, age at first reproduction; LRS, lifetime reproductive success; LRT, likelihood ratio test

Life-history theory predicts that the timing of reproductive events during an individual's life affects its fitness (Cole 1954; Caswell 1982). An early age at first reproduction (hereafter AFR) can increase the number of lifetime reproductive events and shorten generation time, which, in a stable or growing population, should be favored by natural selection (Cole 1954; Bell 1980; Roff 1992; Charlesworth 1994). However, an early AFR may also be costly and reduce future survival or reproductive investment (Lack 1968; Roff 1992; Stearns 1992). Additionally, individuals could benefit from deferring breeding beyond sexual maturity if this enhances parenting skills ('constraint hypothesis': Curio 1983), secures access to higher quality territories or mates ('queuing hypothesis': Zack and Stutchbury 1992; van de Pol et al. 2007), increases reproductive output with age ('restraint hypothesis': Williams 1966; Forslund and Pärt 1995) or decreases reproductive senescence ('senescence hypothesis': Charmantier et al. 2006). If AFR is shaped by natural selection, then individuals should adopt the AFR that is associated with the highest fitness return, which may depend on individual quality and annual variation in environmental conditions.

Individuals of some species express no variation in AFR, while there is a large range in AFR in other species. In the latter case, only certain AFRs are associated with a high lifetime reproductive success (hereafter LRS), but the exact association appears to vary among species (Clutton-Brock 1988; Newton 1989; Oli et al. 2002; Krüger 2005; Charmantier et al. 2006; Millon et al. 2010; Kim et al. 2011; Tettamanti et al. 2012; Zhang et al. 2015). Moreover, the relationship between the species-specific AFR that is associated with the highest LRS (hereafter termed Optimal AFR) and age of sexual maturity can vary across species (Komdeur 1996; Pyle et al. 1997; Oli et al. 2002; Krüger 2005). Yet, the reasons underlying this among-species variation remain unclear as we currently lack comparative studies that investigate the evolution of AFR and deviation in the timing of Optimal AFR during reproductive lifespan across species. Such a study could contribute to our understanding of the general patterns of variation in this crucial life history trait.

Whether species-specific Optimal AFR either approximates or is shifted beyond the age of sexual maturity of the species may depend on interspecific variation in life-history or ecological factors. Across species, the pace of life (i.e. slow or fast life history) is likely to be a major factor influencing variation in AFR and timing of the species-specific Optimal AFR relative to the age of sexual maturity (Roff 1992; Stearns 1992; Charlesworth 1994). A short lifespan should be associated with little or no variation in AFR, and with an Optimal AFR that is close to the species' age of maturity, as any postponement would increase the risk of death before reproduction. In contrast, a long lifespan allows for a larger range in AFR and increases the likelihood of a delayed Optimal AFR, an outcome that is supported by field studies (Pyle et al. 1997; Tettamanti et al. 2012). In addition to lifespan, other life-history, ecological or social traits may influence the deviation from the age of sexual maturity in the species-specific Optimal AFR. Species could benefit from delayed AFR when there is a high level of parental care (e.g. altricial species), or when requiring time to learn specialized skills to survive or reproduce successfully. Conversely, a prolonged association of juveniles with their parents (i.e. family-living; Drobniak et al. 2015) may facilitate skill learning and lead to an earlier species-specific Optimal AFR ('skill hypothesis': Skutch 1961; Langen 1996). An earlier Optimal AFR may also be found in cooperatively-breeding species, since helpers may buffer the reproductive costs of early AFR ('load-lightening hypothesis': Khan and Walters 2002; Santos and Macedo 2011).

Here, we use data from 34 bird species to investigate the extent of variation in reproductive strategies and to assess the potential benefits some species may gain from delaying AFR beyond sexual maturity. We examine interspecific variation in the fitness consequences of AFR using within-species relationships between AFR and a fitness proxy averaged over all individuals within a specific AFR-class. For each of the 34 species, we identified the species- and sex-specific Optimal AFR and several derived metrics, summarized in Table 1, to assess changes in LRS or survival as a function of AFR. Information on species-specific Optimal AFR was previously unavailable for typical meta-analysis approaches due to the substantial challenge of obtaining fitness estimates of populations from several species. Its investigation allows us to make inferences about the selection pressures on AFR that could not be achieved via a simple analysis of interspecific variation in AFR. As a fitness proxy, we used the most commonly provided measure of an individual's productivity, the lifetime number of fledglings or recruits produced (LRS) (Clutton-Brock 1988; Newton 1989 and other references in Table S1). Although it depends on population dynamics, while rate-sensitive fitness estimates (e.g. lambda λ_{ind}) theoretically are more accurate proxies than LRS (Cole 1954; Lewontin 1965; Caswell and Hastings 1980), a number of studies have shown that LRS is a reliable estimate of fitness (Brommer et al. 2002; Link et al. 2002; Dugdale et al. 2010).

Specifically, we addressed the following three questions: (i) How does AFR vary within and among species? (ii) Is variation in AFR associated with differences in LRS, and is the typical AFR of a species the one associated with the highest LRS? (iii) Which life-history (chick developmental mode, LRS and survival change with AFR, lifespan), social (family-living, helper presence) and ecological (latitude, nest predation) factors are associated with among-species variation in deviation of the Optimal AFR from age at maturity? We used a generalized linear mixed model approach in a model selection framework for the analyses, with further control for similarity in phenotype among taxa due to a shared phylogenetic history.

Materials and Methods

DATA COLLECTION

We used data from published (N = 15) and unpublished (N = 21) studies on the age at first reproduction (AFR) and lifetime reproductive success (LRS) for 34 avian species (Table S1). To find published data, we searched online databases (ISI Web of Science, Scopus) using the terms "age at first reproduction", "age at first breeding", or "age at maturity" in combination with "lifetime reproductive success", "lifetime reproductive output", or "fitness" and "avian" or "bird". We included data from long-term studies (years of monitoring exceeding the mean lifespan) in which individuals were followed for a sufficient period to accurately measure LRS (mean duration of study: 20.75 years; range: 8 to 48 years) and where LRS (including its mean, standard deviation and sample size) was reported separately for each category of AFR. We used GetData Graph Digitizer 2.25 (http://www.getdata-graph-digitizer.com/) to extract values from published data that were only presented in figures. Unpublished data were requested from researchers who coordinated long-term monitoring studies.

We collected species-specific data on key life-history, ecological and social lifestyle factors that might influence the effect of AFR on LRS (italicized words represents variable names used in the models), including *chick development mode* (altricial or precocial), *mean lifespan*, *mean body mass*, *latitude*, *nest predation risk*, *family-living* and *helper presence*. We also collected data on the age of maturity for the estimation of an index used as variables in the model (see INDICES AND ESTIMATES). Age of maturity corresponded to the age at which an individual is physiologically able to reproduce, or the minimum age recorded for breeders. Among ecological factors that can contribute to nest predation risk, nest location is well known and important (Martin and Li 1992; Martin 1993). Based on this information, we ordinally ranked the nest predation risk as high risk – ground nesters, medium risk – nests in shrubs, low risk – nests in trees, or very low risk – cavity breeders or species that build their nest floating on water and thus difficult for nest predators to access. We considered species to be family-living when offspring remain with the parents beyond independence and non-family living when juveniles disperse soon after becoming independent (Drobniak et al. 2015). Species were categorized with helper when offspring regularly engage in cooperative breeding and without helper when offspring do not engage in cooperative breeding. Variables not provided for the populations studied were obtained from the Animal Ageing and Longevity database (http://genomics.senescence.info/species/) or the Handbooks of the Birds of the World (del Hoyo et al. 1992-2006).

DATA COMPOSITION

The 34 species included in our study (Figure S1) comprise 10 taxonomic orders and 22 families, with mean lifespan ranging from 1.4 to 18.5 years and mean LRS ranging from 0.67 to 21.16 fledglings produced over the lifetime, or from 0.54 to 2.53 recruits. For blue tits (*Cyanistes caeruleus*) and western gulls (*Larus occidentalis*), we included data from two different populations that were analyzed separately. While age at first reproduction might be influenced by individual quality (Forslund and Pärt 1995; Kim et al. 2011), only few studies provide such information, limiting our ability to include this factor in our analyses. Data collected consisted of average values per species (i.e. body mass) or per AFR age-class category combining data from all cohorts and years. Therefore, annual or cohort variation could not be addressed here but we hope to do so in future work. Note that not controlling for intraspecific individual quality and combining data across cohorts and years is conservative as it reduces the chance of observing biological patterns. Values of mean LRS (N = 34 species) and lifespan (N = 21 species), as well as their standard deviation and sample size (number of individuals), were determined for each AFR age-class category (e.g. from all individuals starting to reproduce at AFR = 1-year old, at AFR = 2, at AFR = 3, and so on), and for each sex if possible. While it would have been more appropriate to use the geometric rather than the arithmetic mean, as it takes into account variability in fitness (see Liou et al. 1993), such data were unavailable. Age at first reproduction was defined as the age at which an individual first reproduced during its life. In most species, this value corresponds to the age when a female laid at least one egg, although in some species the value reflects when a female laid a full clutch. For males, AFR corresponds to the age where its mate laid eggs, and, accordingly, reproductively competent males that failed to acquire a mate were not considered as reproductive at that time. The LRS data were based on the number of fledglings or recruits produced over the lifetime of an individual (Table S1). All LRS values were centered and scaled within species and sexes to convert the original units to those of standard deviations and make them comparable (Schielzeth 2010). For species with only one AFR age-class category, only a single data point was available. Thus we could not estimate the standard deviation necessary for scaling. Instead, we used the standard deviation of the same sex of a species with a similar value of unscaled LRS to calculate the scaled LRS. Accurate estimation of AFR and fitness proxies is challenging as it requires known-aged individuals and intensive individual-based monitoring of reproductive output throughout the lifespan of a representative sample of individuals, as well as data on the survival and reproduction of descendants. Age at first reproduction and fitness proxies may be biased due to extra-pair paternity, or because not all reproductive events of individuals are followed due to emigration from or immigration into the study population.

Consequently, AFR might be overestimated and LRS underestimated for males and overestimated for females. Such biases affect the interpretation of the relationship between AFR and fitness components, and add noise to the data. However, because a relation between AFR and extra-pair paternity and or migration has never been documented, we do not know how and to what extent such a bias would affect our interpretation.

INDICES AND ESTIMATES

Interspecific variation in deviations of the Optimal AFR from the age at sexual maturity might be explained by the association of an early or a late AFR with an increase or a decrease in subsequent survival or reproductive output. However, given the heterogeneity of the data distribution between species and sexes, conventional methods are unable to estimate changes in reproductive output or survival with a changing AFR. Thus, we calculated five derived metrics from the raw data per AFR age-class category to investigate this hypothesis (i.e. average values over all individuals from a specific AFR age-class, combining cohorts and years, for each species and where possible split by sex). These included the Delay Index, which assessed the deviations of the Optimal AFR from the age at sexual maturity, and four indices which assess the relationship between AFR and LRS or survival: the Before Variation Index and the After Variation Index, the Choice Index, and the Lifespan Effect Index (see Table 1).

We visually determined the species-specific AFR that maximized LRS (“Optimal AFR”- Table 1). The use of a single statistical optimization method was not feasible due to the large diversity of patterns in the relationship between AFR and LRS.

Based on the Optimal AFR, the age at sexual maturity and the latest AFR observed within focal species and sex, we assessed the "Delay Index" representing the timing of the Optimal AFR in relation to the reproductive lifespan (illustrated in Table 1):

$$\text{Delay Index} = \frac{\text{Optimal AFR} - \text{maturity age}}{\text{latest AFR} - \text{maturity age}}$$

A Delay Index equal to zero always resulted from the Optimal AFR being the age of maturity.

For 35 out of 62 cases several AFR categories had mean LRS values near that of the Optimal AFR. Hence, we determined the range of the species-specific optimum ages for the onset of reproduction, referred as the "Optimal AFR Range". The Optimal AFR Range included the AFR categories adjacent to the Optimal AFR, with mean LRS values included in the calculation of the standard error bar for the mean LRS of the Optimal AFR (Table 1). The AFR categories forming the Optimal AFR Range are therefore assumed to be similarly beneficial in terms of LRS than the Optimal AFR.

Based on the Optimal AFR Range, we estimated the Before Variation Index and the After Variation Index. These indices correspond to the slope of the relationship between LRS and AFR from the earliest and the latest AFR to the center of the Optimal AFR Range. The slopes were estimated in the whole data set with all AFR age-class categories, and in a data set only including categories with more than 5% or 10% of the individuals (Table 1). Before and After Variation Indices represent the average of the three estimated slopes. We assumed that a delayed AFR should be favored if an early AFR is associated with a lower LRS, while an earlier AFR should be favored if a late AFR is associated with a lower LRS. Therefore, we expected the Delay Index to be positively correlated with the Before Variation Index but negatively with the After Variation Index.

Based on the Optimal AFR Range and the actual value observed for the AFR, we calculated the Choice Index (Table 1), which represented the probability that individuals adopt AFR(s) with highest fitness return:

$$\text{Choice Index} = \frac{\text{Optimal AFR Range}}{\text{number of AFR categories}}$$

In cases with only one AFR category (N = 6 out of 62 cases), the Choice Index was assigned a zero, as in such cases there is no variation in AFR. We assumed that species with a large Optimal AFR Range relative to the number of AFR categories (i.e. with a large Choice Index) would have a lower probability of suffering a LRS cost when initiating reproduction earlier or later than the Optimal AFR. Consequently, such species may have a higher likelihood of benefiting from delayed reproduction than species with only a low number of beneficial AFR. Therefore, we expected the Delay Index to be positively correlated with the Choice Index.

The association between AFR and subsequent survival was calculated via the Lifespan Effect Index, i.e. the correlation coefficient of the reproductive lifespan plotted against AFR per age-class category. We were able to estimate the Lifespan Effect Index for 21 out of 34 species only, due to missing data for mean lifespan for the different AFR age-class categories for 13 species. As causes and consequences cannot be disentangled from a correlation, negative values could indicate a reproductive cost in terms of survival for individuals with a late AFR or an early AFR favored by high intrinsic mortality. By contrast, positive values could indicate a survival cost of early AFR or a late AFR favored by low intrinsic mortality (Table 1, Figure S2). We assumed a survival cost of early AFR to be associated with a late Optimal AFR. Therefore, we expected the Delay Index to be positively correlated with the Lifespan Effect Index.

We verified the robustness of our results based on the indices involving the Optimal AFR Range by considering a second method to estimate it. In this second method, the Optimal AFR Range included AFR(s) adjacent to the Optimal AFR with their 90% CIs overlapping those of the Optimal AFR. The first method (method used in the manuscript abovementioned) represents the logic of a null-hypothesis-like test, which assumes an error distribution around the hypothesis (the Optimal AFR's LRS mean), and if our statistics (the other AFRs' LRS mean) do or do not fall within this range. We also considered this first method to be more straightforward while the use of the second method is more conservative. This is because the use of 90% CI indicates that the LRS population's mean of the focal AFR will fail in 90% of the time, while for the use of the standard error it would do so in around 68% of the time. However, we preferred to present the results from the first method in the manuscript for two reasons. First, most of our data comes from studies with intensive monitoring of a population (Table 1, some of which pretty much sample all individuals in the population) and thus, the LRS means approach the population mean with little error. Second, for some AFRs the LRS estimates were based on a single individual (thus without CI). Note that one could prefer to consider one or the other method depending on their data characteristics and questions.

STATISTICAL ANALYSIS

General procedure

All statistical analyses were carried out in R version 3.0.2 ((R Core Team 2013), http://www.R-project.org/) using linear mixed-effects models (lmer function, lme4 package: Bates et al. 2014) that allow for the non-independence of data from a single species by including species as a random factor in the model. To account for differences in sample size

(N, Table S1) and decrease noise by giving greater emphasis to the more reliable species-specific estimates, all models were weighted (Garamszegi and Møller 2011) by incorporating N-1 in the “weights” argument of the lmer function (Hansen and Bartoszek 2012). Note that removing the weighting did not change the results (Table S2 to S7). To compare coefficients, all continuous predictors were centered (around the mean) and scaled (by the standard deviation) before incorporation in the models (Schielzeth 2010), but we present raw data in the figures. Model assumptions of normality and homogeneity of residuals were checked by visually inspecting histograms and qq-plots of the residuals as well as by plotting residuals against fitted values. For each analysis, we used a model selection process to identify the predictors that best explained variation in the response variable. Model selection was based on minimization of the corrected Akaike's information criterion (AICc) (Burnham and Anderson 2011). Support for an effect of an explanatory variable on the response variable was based on comparison of AICc values between the full model with the effect of interest included vs. excluded, and when ΔAICc ($AICc_{included} - AICc_{excluded}$) was less than or equal to minus five (Burnham and Anderson 2011). The 95% confidence interval (CI) of the predictor estimates was obtained using the confint function (stats package: R Core Team 2013).

The influence of phylogenetic similarity among species was tested in the “best model” obtained during the lmer model selection process (model including only explanatory variables with ΔAICc ≤ -5). This was done by running a phylogenetically controlled mixed-effects model in ASReml-R (VSN International, Hempstead, U.K.; www.vsn-intl.com) with the same set of predictors as the lmer “best model” for each analysis. The phylogeny was included as a random effect in the form of a correlation matrix of distances from the root of the tree to the most recent common ancestor between two species. The phylogenetic effect was tested by performing a REML likelihood ratio test (comparing the REML likelihood of the same ASReml model with and without phylogeny; the log-likelihood ratio test statistic was assessed against a χ^2 distribution with one degree of freedom). The phylogenetic tree used in this comparative study was adapted from a recent species-level molecular phylogenetic assessment (Jetz et al. 2012; Ericson backbone phylogeny) (Figure S1).

Variation in age at first reproduction

To determine how AFR varied within and among species, we noted how often an AFR was the most frequently observed AFR within a species (mode) (Figure S3A) and considered the frequency of a specific AFR age-class across all species (Figure S3B). Then, mean AFR and its standard deviation were calculated for each of the 34 species. We tested the influence of sex, mean lifespan and social lifestyle (family-living and presence of helpers) on variation in mean AFR across the 24 species for which we had data for both sexes (Table S1). We used a weighted linear mixed-effect model with population mean AFR as the unit of analysis, and included species as a random effect. Since AFR cannot exceed the mean lifespan, AFR and mean lifespan should be correlated positively. Therefore, we tested whether the estimated correlation between AFR and mean lifespan differed significantly from the null expectation. To do so, we performed a conservative permutation analysis (following Charmantier et al. 2006; Lane et al. 2011). For each mean lifespan, a mean AFR value was randomly selected with replacement from our dataset. During re-sampling we fixed the rule that AFR was smaller than mean lifespan. Data were re-sampled 500 times and analyzed using the same weighted linear mixed-effect model as described above. We estimated the average estimates and 95% CIs over the 500 model outputs and compared them to those observed.

Fitness consequences of age at first reproduction

To determine whether variation in AFR has consequences for LRS, the correlation between AFR and LRS (within-species) as well as its average influence (among-species effect) was investigated using within-subject centering (van de Pol and Wright 2009). The within-species effect was calculated for each sex and species by subtracting the species- and sex-specific mean AFR from each AFR age-class category observed within sex and species (within-species AFR effect; van de Pol and Wright 2009). The among-species effect was determined as the mean AFR within sex and species (between-species AFR effect; van de Pol and Wright 2009). To test for non-linear effects of AFR on LRS within species, a quadratic term of the within-species AFR effect was included in the model. The AFR values were centered to reduce collinearity between the within-species AFR effect and the within-species AFR^2 effect. Centering enabled independent interpretation of the linear and the curvature effect (Schielzeth 2010). Due to apparent interspecific variation in the relationship between AFR and LRS, the ideal analytical framework would have been a random intercept and slope model that estimated separate intercepts and slopes for each species. However, our sample size did not provide sufficient power to support such a model (Martin et al. 2011; van de Pol 2012). Therefore, we ran a standard weighted linear mixed-effect model using the average LRS within AFR age-class categories, with sex and population as units of analysis. Species was included as a random effect in this analysis, along with the natural log of mean body mass as a covariate. We included lifespan in this model as a covariate, since reproductive performance corrected for survival estimates approximates real fitness better (Roff 1992). While the output of the analysis with and without lifespan were similar, lifespan is strongly correlated with the between-species AFR effect. Therefore, we present the analysis without lifespan to avoid issues caused by collinearity (Dormann et al. 2013).

To assess whether the most frequently observed AFR within each species was an optimal strategy, the AFR mode within each species was correlated with the AFR that maximized LRS (i.e., Optimal AFR, Table 1). Then, the species-specific Optimal AFR was compared to the age at sexual maturity to identify species with optimal delayed reproduction (i.e., species with Optimal AFR > Age at maturity). Finally, the Optimal AFR was correlated with lifespan to identify if a benefit from delaying the onset of reproduction beyond sexual maturity coincided with long lifespan.

Among-species variation in the relative timing of optimal age at first reproduction

We used a model selection and model averaging approach (Grueber et al. 2011) to determine the factors that explain interspecific variation in deviations of the Optimal AFR from the age of sexual maturity (i.e., Delay Index, Table 1). All life-history, social and ecological factors listed above were included (see DATA COLLECTION), as well as indices reflecting the relationship between LRS and AFR: the Choice Index, and the Before and After Variation Indices (see above, Table 1). In a second analysis, the Lifespan Effect Index was included for the 21 species for which we had detailed data on lifespan mean for each AFR age-class category (Table 1, Figure S2). Due to reduced statistical power of the latter (as on restricted dataset, see above), in the results section we present only the estimates and 95% CI of the analysis excluding the Lifespan Effect Index. Each of the before mentioned variables, and the biologically relevant interactions (Before Variation Index x After Variation Index, Choice Index x Before Variation Index, Choice Index x After Variation Index, Choice Index x Family-living, Choice Index x Helper presence, Mean lifespan x Family-living, Mean lifespan x Helper presence, Nest predation risk x Family-living, Nest predation risk x Helper presence; Table S8 lists predictions associated with these interactions) were tested against the Delay Index in a weighted linear mixed-effect models with Delay Index for each sex and population as a unit of analysis. Species was added as a random effect. Sex and the natural logarithm of body mass were included as default fixed-effects variables to control for allometry and any differences between sexes. Due to a large number of possible combinations between all predictors, we used the R package MuMIn (Barton 2013) to perform model selection. The candidate model set included models with Δ AICc ≤ 5, Δ AICc being the AICc of the focal model minus the AICc of the best model (see Table S9 for analysis excluding Lifespan Effect Index and Table S10 for analysis including Lifespan Effect Index). To estimate the relative importance of a factor, we summed the Akaike's weights of the models in the set of best models including the focal factor, following the method described by Symonds and Moussalli (2011).

Results

VARIATION IN AGE AT FIRST REPRODUCTION

Across species (N = 34), age at first reproduction (AFR) ranged from one to 20 years. In 11 species, the modal AFR was one year (Figure S3A). In 70% of species, AFR was age 3 or less and only 20% of species had an AFR that was greater than 6 years of age (Figure S3B). Within species, the number of AFR categories ranged from one to 15 (average = 4.8 years; SD = 3.1; N = 34) and the mean AFR and its standard deviation varied among species (Figure 1). Removing sex or social variables (i.e. family-living, helper presence) from the model did not influence mean AFR (Table 2). However, mean AFR correlated positively with mean lifespan (parameter estimate for mean lifespan = 0.87, 95% CI (hereafter given in brackets after all estimates): 0.72 to 1.02, Table 2), and this correlation exceeded that expected from the mathematical interdependence of AFR and mean lifespan (estimated by the permutation test: mean of 500 simulations: 0.63 (0.87 to 0.79), Δ AICc = -22.24). A positive relationship between AFR and mean lifespan was also apparent when comparing the AFR age-class categories within each species (Figure 2). The phylogenetic effect on mean AFR was significant (likelihood ratio test: LRT = 6.99, df = 1, $p < 0.01$).

FITNESS CONSEQUENCES OF AGE AT FIRST REPRODUCTION

Our within-subject centering approach revealed no among-species effect of AFR on LRS, but a within-species effect of both AFR and AFR^2 (Figure 3). Within species, there was strong directional selection for an early AFR (within-species AFR effect estimate = -0.54 (-0.70 to -0.39), Table S11), as well as stabilizing selection (within-species AFR^2 effect estimate = -0.26 (-0.43 to -0.10), Table S11) (Figure 3). The phylogenetic effect on mean LRS for the corresponding AFR was not significant (likelihood ratio test: p = 1). Twenty-six out of 34 species (76%) had an Optimal AFR delayed beyond the age at maturity, and this delay correlated positively with a longer mean lifespan (slope = 0.28, $r_{Spearman}$ = 0.61, $p < 0.005$; Figure 4). Both the most-observed AFR and mean AFR correlated with the AFR with the highest LRS (Optimal AFR vs. modal AFR: slope = 0.98, $r_{Spearman}$ = 0.80, $p < 0.0001$; Optimal AFR vs. mean AFR: slope = 0.95, $r_{Spearman}$ = 0.84, $p < 0.0001$). The latter was true even when only looking at species with a large number of observed AFR age-class categories (Table S12).

AMONG-SPECIES VARIATION IN THE RELATIVE TIMING OF OPTIMAL AGE AT FIRST REPRODUCTION

While the Delay Index was associated with indices that reflect a change in LRS and survival as a function of AFR (i.e. Choice, Before Variation and Lifespan Effect Indices; Table 1, all predictor weights ≥ 0.45), it was only marginally related to social (predictor weights < 0.45) or ecological factors (predictor weights ≤ 0.30; Tables 3 and 4). A delayed optimal onset of reproduction (i.e. large Delay Index) was found in species with a large range of optimal AFR relative to reproductive lifespan (Choice Index: estimate = 0.44 (0.15 to 0.72), Table 3). Moreover, a large Delay Index was found in species in which early AFR was associated with a decreased LRS (Before Variation Index estimate = 0.30 (0.07 to 0.54), Table 3 and Figure 3) and a reduced reproductive lifespan (Lifespan Effect Index estimate = 0.54 (0.37 to 0.72), Table 4). Finally, larger species showed later optimal onset of reproduction than smaller species (ln (body mass) estimate: 0.35 (0.01 to 0.69), Table 3). These results remained quantitatively similar when using indices estimated with the Optimal AFR Range determined under the criterion where AFR categories included in the Optimal AFR Range were AFR(s) adjacent to the Optimal AFR with their 90% CIs overlapping those of the Optimal AFR (Tables S13 to S16).

Discussion

Age at first reproduction (AFR) is a key life-history parameter with consequences for individual reproductive output, and hence its effect on fitness has been studied in a number of intraspecific studies (see references in Table S1). Here we provide a first comparative analysis using a representative amount of averaged within-species information to examine interspecific variation in the relationship between AFR and lifetime reproductive success (LRS). Identifying the species-specific AFR that results in the highest LRS (i.e. Optimal AFR) allowed us to investigate not only within- and among-species variation in the relationship between AFR and LRS, but also differences in the benefits and costs associated with variable timing in the onset of reproduction among species. Our results demonstrated that the most commonly observed AFR within a species corresponds to the species-specific Optimal AFR. Among species, Optimal AFR varied considerably. This study showed that lifespan was a major predictor of the relative timing of the Optimal AFR within the reproductive lifespan and that they correlated positively. Additionally, our analyses revealed that Optimal AFR beyond the age of maturity was associated with a decrease in fitness and survival that arose from starting to reproduce at earlier ages than the Optimal AFR.

Age at first reproduction varied considerably both within and among species (Figure 1). Some species displayed no variation in AFR (e.g. long-tailed tit *Aegithalos caudatus*, indigo bunting *Passerina cyanea*, common buzzard *Buteo buteo*), while others exhibited large variation (e.g. mute swan *Cygnus olor*, wandering albatross *Diomedea exulans*, eurasian oystercatcher *Haematopus ostralegus*). Most species that expressed variation in AFR experienced negative consequences for LRS from initiating reproduction either too early or too late in life (e.g. the Optimal AFR was at an intermediate point in the reproductive lifespan: between the age of sexual maturity and the oldest AFR observed within a population), while for others the earliest or latest observed AFR resulted in the highest LRS (Figure 3). This suggests simultaneous directional and stabilizing selection. If the pattern observed is a footprint of selection acting at the individual level, this should lead to a decrease in average AFR and a reduction in its evolvability. However, a comparative study directly investigating individual variance would be needed to assess this hipothesis.

While there was no overall interspecific relationship between AFR and LRS, a within-species relationship between AFR and LRS (Table S11) indicates that evolutionary processes operate at different scales. On the one hand, large-scale evolution acts on all individuals within a population, which might confound the detection of a relationship between AFR and LRS. On the other hand, local-scale evolution acts on individuals, such as on variation in individual quality (Van Noordwijk and De Jong 1986; Kim et al. 2011), food availability (Brommer et al. 1998), territory quality (Krüger 2005), population density (Krüger 2005) or climatic conditions (Gibbs and Grant 1987; Kim et al. 2011), which also might drive the relationship between AFR and LRS. Differences among cohorts in the relationship between AFR and LRS (Brommer et al. 1998; Kim et al. 2011) might additionally explain the absence of a between-species effect of AFR on LRS, but our data did not allow us to take potential differences in individual or cohort quality into account.

Among-species variation in mean AFR correlated positively with lifespan (Table 2), supporting the life-history paradigm that the pace of life fundamentally affects reproductive timing (Roff 1992; Stearns 1992; Charlesworth 1994). Furthermore, the species-specific optimal reproductive strategy varied among species, where species with a mean lifespan of up to six years (median mean lifespan: 1.9 years) had an Optimal AFR of one year, providing a quantitative benchmark to differentiate between short- and long-lived bird species. At the other extreme, species with a longer lifespan had a later mean AFR (Table 2) and a later Optimal AFR (Figure 4).

When relating the position of the Optimal AFR to the age of sexual maturity of a species, our results revealed that the Optimal AFR was beyond the age of maturity in 26 of 34 species. Thus, individuals in these species appear to benefit from delaying their onset of reproduction (e.g. female tawny owl *Strix aluco* (Millon et al. 2010); female goshawk *Accipiter gentilis* (Krüger 2005); sexes combined short-tailed shearwater *Puffinus tenuirostris* (Wooller et al. 1989)). The association of an Optimal AFR beyond the age of sexual maturity with a long mean lifespan suggests that the positive effect of lifespan on mean AFR is not caused by physiological constraints associated with maturity. Indeed, longer-lived species mature later and still adopt an AFR past their age of maturity, and they experienced a larger

LRS as a consequence (Figure 4). Such a benefit from delayed AFR until after the age of sexual maturity was found not only in long-lived species, but also in six out of 11 short-lived species with a mean lifespan of less than three years (Figure 4).

When controlling for reproductive lifespan, we found that interspecific variation in deviation of the Optimal AFR from the age at maturity was primarily associated with a change in survival and fitness with AFR (Tables 3 and 4). Moreover, our results confirmed that an early AFR might be favored by a short reproductive lifespan and vice versa (Roff 1992; Stearns 1992; Charlesworth 1994) (Table 4 and Figure 2). Species in which an early onset of reproduction was associated with a reduced reproductive lifespan benefited from delaying AFR (Table 4 and Figure S2), which supports the restraint hypothesis (Williams 1966; Forslund and Pärt 1995). Moreover, the cost of early reproduction, measured as a decrease in LRS relative to the optimum, correlated positively with the optimal delayed reproductive onset (Table 3). An early reproductive onset might be costly because of differences in individual competitive ability, if this early onset leads to unequal probabilities of acquiring a high-quality territory (Ens et al. 1995; Ekman et al. 2001; Prevot-Julliard et al. 2001; Cooper et al. 2009) or to high physiological costs (Hawn et al. 2007). This pattern suggests that different factors affect the evolution of sexual maturity and the onset of reproduction. Interestingly, in species where there was limited change in LRS relative to AFR, postponing the onset of reproduction beyond sexual maturity was chosen over other earlier AFR leading to similar fitness. Therefore, not reproducing as soon as physiologically capable might provide further benefits. Our results provide empirical support for the hypothesis that costs of reproduction shape the onset of reproduction (Lack 1968; Roff 1992; Stearns 1992).

It has been argued that variation in AFR might be sub-optimal, reflecting constraints on early breeding, such as limited access to high-quality mates or to high-quality breeding sites (Lack 1968; Emlen 1982; Stearns 1989; Koenig et al. 1992). However, our results suggest that the onset of reproduction most likely is an optimal strategy, since the most commonly observed AFR coincides with the Optimal AFR. A number of theories developed to explain the evolution of cooperative breeding depicts the decision of offspring to remain with their parents beyond sexual maturity as a "best of a bad job" strategy that reflects dispersal constraints (Emlen 1982; Koenig et al. 1992; Arnold and Owens 1998; Hatchwell and Komdeur 2000). The lack of a strong correlation between the Delay Index and the different social lifestyles suggests that delayed onset of reproduction might not have evolved due to constraints (Ekman et al. 2004; Ekman 2007), but instead constitutes a beneficial life-history decision, which correlates positively with lifespan (Covas and Griesser 2007). Still, the lack of a correlation between social factors and variation in the optimal timing of reproduction could reflect the fact that our data is skewed towards pair-breeding, northern hemisphere species. Including more tropical and southern hemisphere species might alter our results and magnify the role of social factors in our analyses, as the latter two groups are often long-lived (Valcu et al. 2014), stay longer with their parents (Russell 2000) and are more likely to breed cooperatively (Jetz and Rubenstein 2011). The current paucity of long-term studies in these regions potentially biases our view of life-history evolution (Martin 2004).

Although we found no significant effect of sex in our study, the relationship between AFR and LRS, and the optimal timing of reproduction, sometimes differed between sexes (Figures 3 and S4). Twelve out of 24 species showed sex-specific differences in the Delay Index; females benefited more from earlier onset than males in seven species, whereas the opposite was true in five species (Figure S4). Intraspecific studies have demonstrated sex differences in the relationship between LRS and AFR (e.g. western gull *Larus occidentalis* (Pyle et al. 1997); green woodhoopoe *Phoeniculus purpureus* (Hawn et al. 2007); blue-footed booby *Sula nebouxii* (Kim et al. 2011)), highlighting the need to consider sex-specific variation in life-history traits (McDonald 1993; Santos and Nakagawa 2012). The positive correlation between the relative timing of Optimal AFR and body mass concurs with findings in mammals where AFR is correlated strongly with body mass (larger mammals having later AFR; Estern 1979; Wootton 1987). Nevertheless, we additionally demonstrated that, in birds, larger species benefited more from delaying the onset of reproduction beyond sexual maturity than smaller species. Therefore, body mass seems to be an important factor associated with variation in reproductive strategy. Animals with a large body size invest substantial amounts of resources into growth. Although, in birds, growth after sexual maturity is negligible (Ricklefs 1983), postponing the onset of reproduction might counterbalance the cost endured during the development phase and increase the probability of a high lifetime reproductive output.

In conclusion, AFR varies both within and among species, and this variation is reflected in LRS. The most frequently observed AFR within a species results in the highest LRS. Where an AFR delayed beyond physiological maturity co-occurred with the highest LRS, this delay was mainly associated with a long lifespan and a decrease in LRS and future survival linked to early reproduction. Our study is the first to provide empirical confirmation of several key predictions of life-history theory across species that lifespan and costs of reproduction shape reproductive timing (Lack 1968; Roff 1992; Stearns 1992; Charlesworth 1994). Moreover, the finding that, in long-lived species, postponing the onset of independent reproduction is an optimal strategy has important implications for long-held perspectives on the evolution of sociality. Hitherto, the decision of young birds to remain with their parents and become helpers has been viewed as a sub-optimal response to the lack of breeding opportunities (Emlen 1982; Koenig et al. 1992; Arnold and Owens 1998). Our results clearly indicate that this decision can be a strategy to mitigate the costs of early reproduction. Overall, our results are consistent with life-history theory and challenge current theories on the evolution of family formation and cooperative breeding.

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Conflict of Interest

We have no conflict of interest.

Author contributions

P.B., S.B., R.B., A.C., C.C., R.E., M.H., H.H., O.K., J.M., A.M., S.N., R.P., A.N.R., A.R., J.T., J.V., M.V.P., I.G.W., I.S.W., A.W. provided unpublished data on lifetime reproductive success. E.M. compiled the data, performed the statistical analysis and wrote the first draft of the manuscript. All authors contributed to revisions (especially M.G.) and gave final approval for publication. M.G. helped with data compilation and reflection on the manuscript. S.M.D., S.N. and M.G. helped with the statistical methods and estimation of the indices. S.M.D. wrote the R script to automate the estimation of two indices.

Data accessibility

The datasets supporting this article have been uploaded as part of the Supporting Information.

Table 1. Definitions and descriptions of the parameters and indices estimated for each sex (when possible) and each species followed by a graph illustrating the description based on the case of the Eurasian sparrowhawk (*Accipiter nisus*). See also *Indices and estimates* section in *Materials and Methods*.

Species parameter	Definition	Biological description	Technical description
Optimal AFR	AFR that results in the highest LRS	Reflects the species-average optimum strategy of onset of reproduction	AFR that maximizes mean LRS excluding AFR categories with <10% individuals. Extracted visually
Optimal AFR Range	Range of optimal AFR(s)	Reflects the range of the species-average optimum strategy of onset of reproduction	Number of AFR(s) adjacent to the Optimal AFR with mean LRS values overlapped by the standard error bars of the Optimal AFR. Extracted visually. Range from 1 to 15
Before Variation Index	LRS cost of initiating reproduction before the Optimal AFR Range	Reflects the LRS cost of adopting a reproductive strategy which is earlier than the range of species-average optimum strategy of onset of reproduction	Slope before the Optimal AFR Range (center of the range) between mean LRS and AFR; Average of slopes obtained when all individuals were included, when excluding AFR categories with <5% and <10 % individuals (mean standard error slope = 0.21). A large positive value indicates a strong negative fitness impact of reproducing before the Optimal AFR Range
After Variation Index	LRS cost of initiating reproduction after the Optimal AFR Range	Reflects the LRS cost of adopting a reproductive strategy which is later than the range of species-average optimum strategy of onset of reproduction	Slope after the Optimal AFR Range (center of the range) between mean LRS and AFR; Average of slopes obtained when all individuals were included, when excluding AFR categories with <5% and <10 % individuals (mean standard error slope = 0.18). A large negative value indicates a strong negative fitness impact of reproducing after the Optimal AFR Range
Delay Index	Relative position of the Optimal AFR during the reproductive lifespan	Reflects when – during the average-reproductive lifespan of a species – individuals from a species benefit the most from initiating their reproduction	Varies between 0 and 1. Delay Index 0: the optimal strategy is to start reproduction at physiological maturity; Delay Index 1: the optimal strategy is to delay the onset of reproduction to maximum AFR
Choice Index	Range of optimal AFR(s) relative to the number of AFR observed	Reflects the species-average span of "beneficial choice" in AFR, (i.e. AFRs leading to higher LRS)	Varies between 0 and 1. Choice Index of 0: species has only one optimal AFR; Choice Index of 1: all AFR are optimal
Lifespan Effect Index	Effect of AFR on the mean reproductive lifespan (for each AFR category: see Figure S2)	Reflects the species-specific average effect of the onset of reproduction on survival	Correlation coefficient between mean reproductive lifespan and AFR (Fisher's z transformed) (Koricheva et al. 2013). Positive values suggest a cost of early onset of reproduction, while negative values suggest a cost of late onset

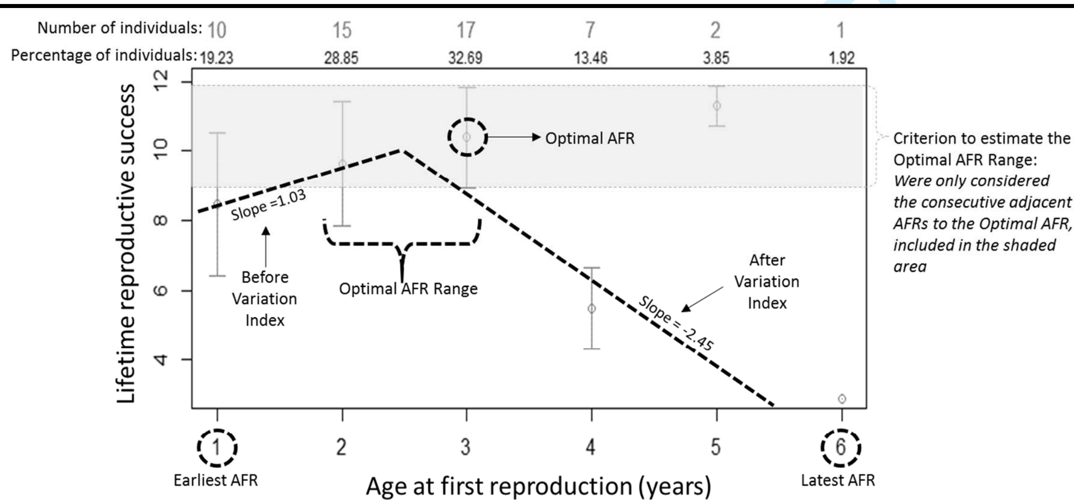


Table 2. Effect of sex, mean lifespan of species, family-living and presence of helpers on mean AFR within a species (N = 26 populations, 24 species for which data were available for both sexes). Estimates and 95% confidence intervals (CI) are presented. Δ AIC_c corresponds to the change in AIC_c when the specific parameter was included vs. excluded from the full model.

	Standard deviation	Estimate	95% CI	Δ AIC_c
Fixed effects:				
intercept		0.10	(-0.14, 0.34)	-
sex: Female		0.00	na	-2.51
sex: Male		0.03	(0.01, 0.05)	
mean lifespan $_{species}$*		0.87	(0.72, 1.02)	-61.65†
family-living: NO		0.00	na	2.58
family-living: YES		-0.12	(-0.89, 0.64)	
helper presence: NO		0.00	na	2.08
helper presence: YES		-0.33	(-1.16, 0.50)	
Random effects:				
species	0.52		(0.40, 0.70)	
residuals	0.93		(0.72, 1.26)	

* factor centered and scaled; na – not applicable; † support for inclusion of the factor

Table 3. Relative importance of predictors included in the full model for the analysis of Delay Index variation excluding Lifespan Effect Index (N = 36 populations, 34 species) and model averaging estimates (based on 53 models with Δ AICc ($AICc_{focal\ model} – AICc_{best\ model}$) ≤ 5, see Table S9).

Predictors	**Predictor weight***	**Relative importance of predictors†**	**Model averaging estimates‡,§**	**95% CI**
intercept			0.14	(-0.71, 1.00)
ln(body mass)	0.49	1.00	0.35	(0.01, 0.69)
sex	0.49	1.00	Both: 0.00 Female: -0.06 Male: -0.24	na (-0.94, 0.82) (-1.12, 0.65)
Choice Index ¶	0.49	1.00	0.44	(0.15, 0.72)
Before Variation Index ¶	0.48	0.98	0.30	(0.07, 0.54)
family-living	0.40	0.82	NO: 0.00 YES: 0.01	na (-1.45, 1.48)
helper presence	0.40	0.82	NO: 0.00 YES: 0.49	na (-2.12, 3.31)
nest predation risk	0.28	0.56	0.03	(-0.34, 0.43)
Choice Index: helper presence	0.25	0.51	NO: 0.00 YES: -0.67	na (-2.45, -0.18)
mean lifespan	0.25	0.50	0.09	(-0.26, 0.60)
Choice Index: family-living	0.23	0.46	NO: 0.00 YES: 0.57	na (-0.50, 3.00)
mean lifespan: helper presence	0.22	0.44	NO: 0.00 YES: 2.48	na (2.66, 8.49)
mean lifespan: family-living	0.21	0.43	NO: 0.00 YES: -1.91	na (-6.12, -2.72)
nest predation risk: family-living	0.21	0.43	NO: 0.00 YES: 0.91	na (1.23, 2.97)
Before Variation Index: Choice Index	0.17	0.35	0.13	(-0.08, 0.82)
After Variation Index ¶	0.14	0.28	-0.04	(-0.37, 0.05)
nest predation risk: helper presence	0.10	0.21	NO: 0.00 YES: -0.41	na (-3.82, -0.13)
chick development mode	0.05	0.11	Altricial: 0.00 Precocial: -0.02	na (-1.20, 0.74)
latitude	0.03	0.07	-0.01	(-0.41, 0.23)
Before Variation Index: After Variation Index	0.00	0.01	0.00	(-0.08, 0.19)

*: sum of model weights from Table S9 including the focal predictor. na – not applicable;
†: predictor weight relative to the highest weighted predictor.
‡: model averaging estimates according to full model averaging approach since the best AIC_c model is not strongly weighted (weight = 0.05) (Symonds and Moussalli 2011).
§: reference levels of categorical variables have an estimate of 0; estimates reflect difference in slope between the reference level and focal level.
Note: The relative importance of body mass and sex is due to their inclusion by default in each model to control for allometry and sex differences. All continuous variables are centered and scaled.
¶: predictors reflecting the relationship between LRS and AFR, see Table 1 and the Indices and estimates section of Materials and methods.

Table 4. Relative importance of predictors included in the full model for the analysis of Delay Index variation including Lifespan Effect Index (N = 22 populations, 21 species) and model averaging estimates (based on 28 models with Δ AICc ($AICc_{focal\ model} - AICc_{best\ model}$) ≤ 5, see Table S10).

Predictors	Predictor weight*	Relative importance of predictors†	Model averaging estimates‡,§	95% CI
intercept			0.42	(-0.34, 1.18)
ln(body mass)	0.57	1.00	0.36	(-0.23, 0.95)
sex	0.57	1.00	Both: 0.00	Na
			Female: -0.67	(-1.43, 0.09)
			Male: -0.35	(-1.11, 0.42)
Choice Index ¶	0.57	1.00	0.35	(0.17, 0.52)
Lifespan Effect Index ¶	0.57	1.00	0.54	(0.37, 0.72)
After Variation Index ¶	0.38	0.66	-0.20	(-0.56, -0.05)
helper presence	0.26	0.46	NO: 0.00	Na
			YES: 0.56	(0.03, 2.40)
family-living	0.24	0.42	NO: 0.00	Na
			YES: -0.32	(-1.59, 0.08)
mean lifespan	0.23	0.41	0.20	(-0.01, 0.98)
chick development mode	0.10	0.17	Altricial: 0.00	Na
			Precocial: -0.11	(-1.28, 0.04)
nest predation risk	0.10	0.17	0.06	(-0.08, 0.74)
latitude	0.07	0.13	0.02	(-0.32, 0.56)
Choice Index: family-living	0.04	0.07	NO: 0.00	Na
			YES: 0.03	(-0.14, 0.87)
Choice Index: helper presence	0.04	0.07	NO: 0.00	Na
			YES: 0.03	(-0.18, 1.07)
Before Variation Index ¶	0.03	0.06	0.01	(-0.16, 0.35)

*: sum of model weights from Table S10 including the focal predictor. na – not applicable;
†: predictor weight relative to the highest weighted predictor.
‡: model averaging estimates according to full model averaging approach since the best AIC_c model is not strongly weighted (weight = 0.10) (Symonds and Moussalli 2011).
§: reference levels of categorical variables have an estimate of 0; estimates reflect difference in slope between the reference level and focal level.
Note: The relative importance of body mass and sex is due to their inclusion by default in each model to control for allometry and sex differences. All continuous variables are centered and scaled.
¶: predictors reflecting relationship between LRS or survival and AFR, see Table 1 and the Indices and estimates section of Materials and methods.

Figure legends

Figure 1. Mean AFR (years) and standard deviation for all 36 populations (34 species) (both sexes combined). Mean AFR ranged from 1 to 12.8 years (mean ± SD = 3.0 ± 2.6, N = 36), and standard deviation from 0 to 2.31 (mean ± SD = 0.80 ± 0.58, N = 36). A number after the name of a species indicates different populations.

Figure 2. Relationship between AFR (years) and the associated mean lifespan within species and sexes (years, N = 22 populations (21 species) for which detailed data on mean lifespan per AFR category were available). Each point is the mean lifespan of individuals within each AFR category. A number after the name of a species indicates different populations. Regression lines are based on the raw data and were drawn for all cases independent of whether the correlation was significant or not.

Figure 3. Variation in AFR and consequences on fitness - Relationship between standardized LRS and AFR for the 36 populations of the 34 species, separated by sex where possible (a point is the mean LRS (centred and scaled) over all individuals that started to reproduce at a specific AFR). Curves represent quadratic fit of the relationship between standardized LRS and AFR independent of whether the relationship was significant or not.

Figure 4. Species-specific Optimal AFR presented relative to the species age at maturity (left y-axis) with species ordered by mean lifespan (both sexes combined). Mean lifespan values are represented by the grey line and the right y-axis. A number after the name of a species indicates the different populations included in the study.

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Information on the source and the type of LRS data for each study

Table S2. Model without weighting – Variation in AFR analysis

Table S3. Model without weighting – Fitness consequence of AFR analysis

Table S4. Model without weighting – Delay Index analysis excluding Lifespan Effect Index

Table S5. Model without weighting – Delay Index analysis including Lifespan Effect Index

Table S6. Model without weighting – Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index

Table S7. Model without weighting – Model selection output for the analysis of Delay Index variation including Lifespan Effect Index

Table S8. Justification for the interactions used in the analysis of the Delay Index

Table S9. Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index

Table S10. Model selection output for the analysis of Delay Index variation including Lifespan Effect Index

Table S11. Fitness consequence of AFR analysis

Table S12. Correlation between Optimal AFR vs. modal AFR and mean AFR for different sest of species

Table S13. Model with 90CI Indices – Delay Index analysis excluding Lifespan Effect Index

Table S14. Model with 90CI Indices – Delay Index analysis including Lifespan Effect Index

Table S15. Model with 90CI Indices – Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index

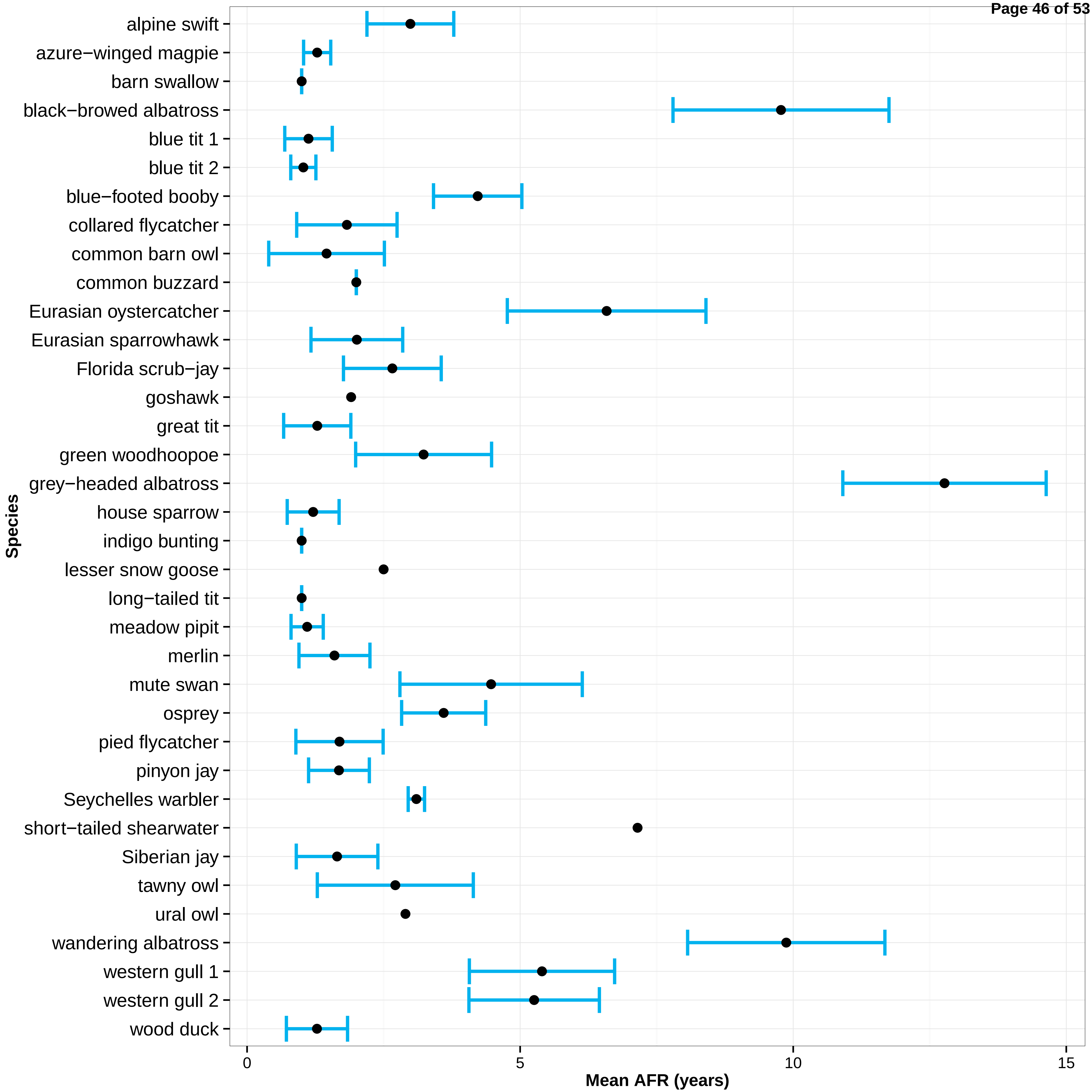
Table S16. Model with 90CI Indices – Model selection output for the analysis of Delay Index variation including Lifespan Effect Index

Figure S1. Phylogenetic tree

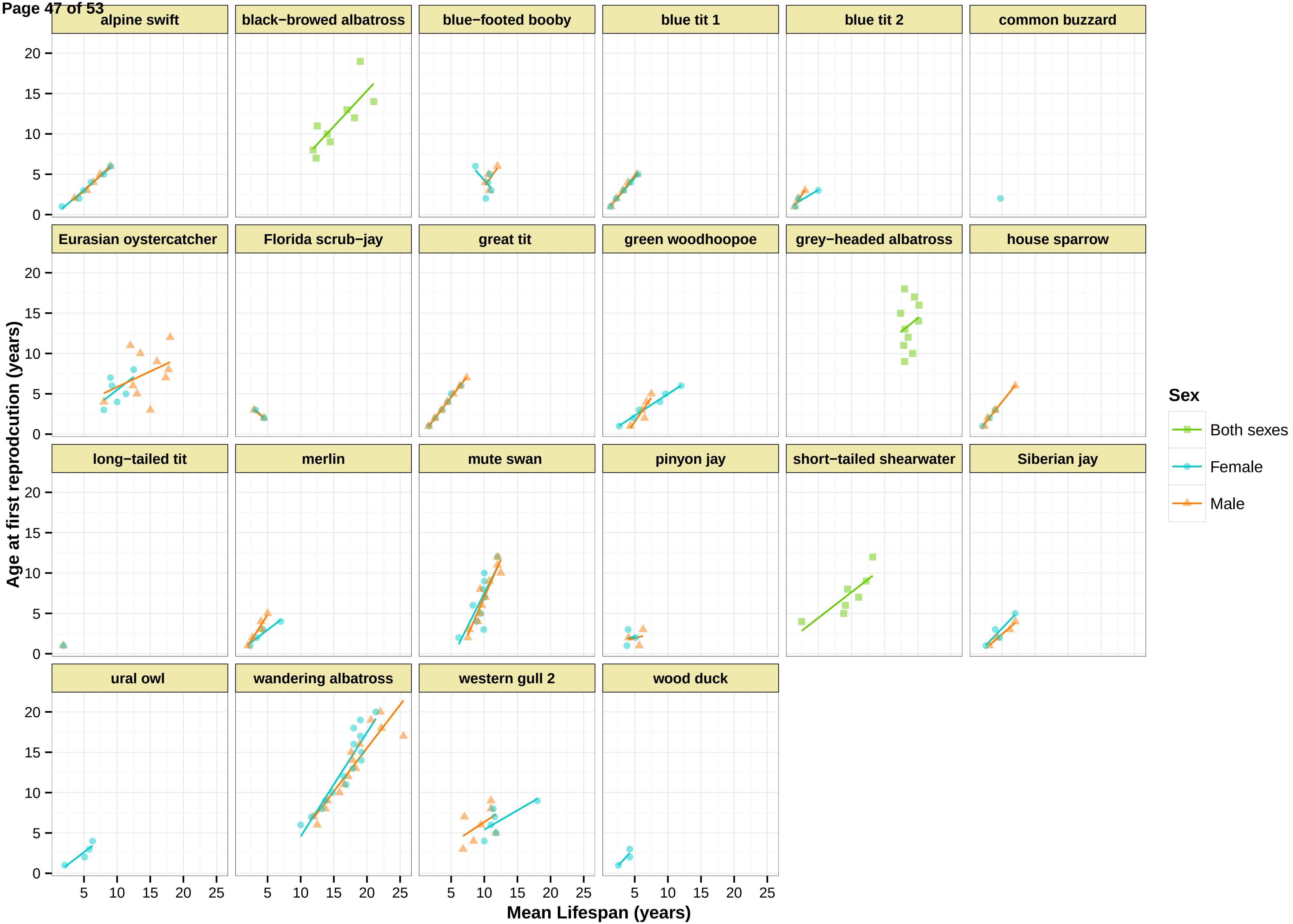
Figure S2. Variation in AFR and consequences on mean reproductive lifespan

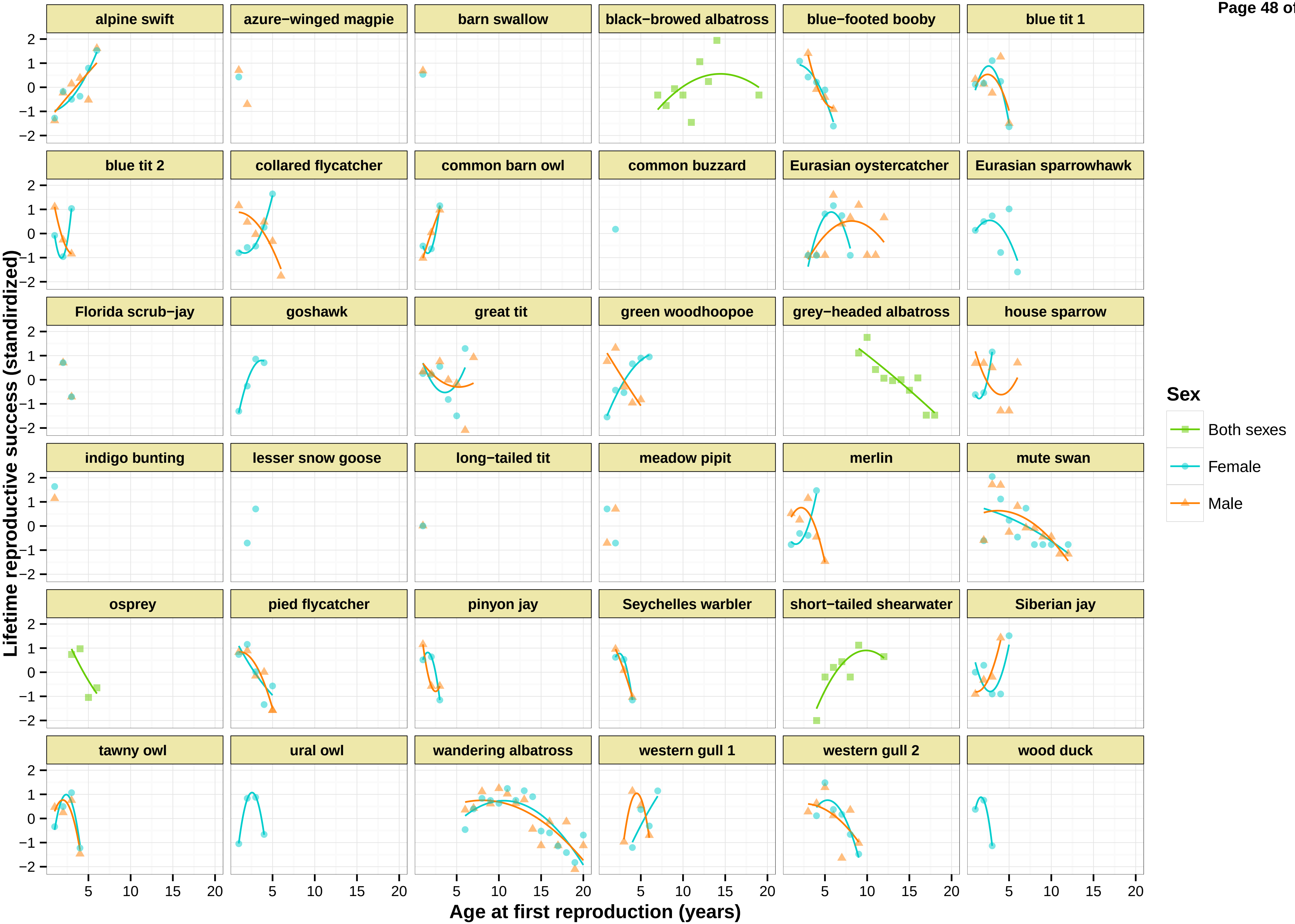
Figure S3. Variation in AFR

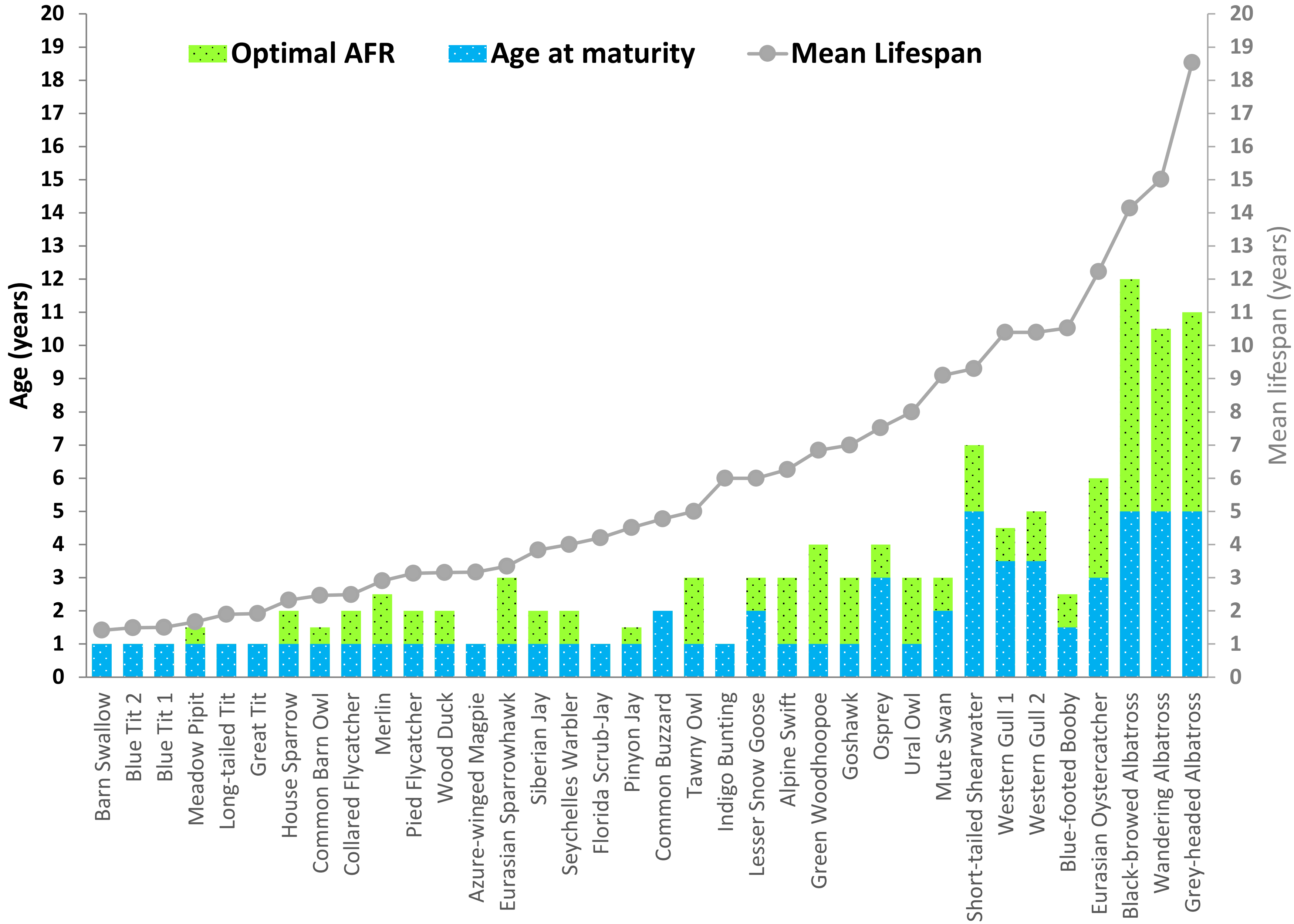
Figure S4: Sex differences in the Delay Index



alpine swift
azure−winged magpie
barn swallow
black−browed albatross
blue tit 1
blue tit 2
blue−footed booby
collared flycatcher
common barn owl
common buzzard
Eurasian oystercatcher
Eurasian sparrowhawk
Florida scrub−jay
goshawk
great tit
green woodhoopoe
grey−headed albatross
house sparrow
indigo bunting
lesser snow goose
long−tailed tit
meadow pipit
merlin
mute swan
osprey
pied flycatcher
pinyon jay
Seychelles warbler
short−tailed shearwater
Siberian jay
tawny owl
ural owl
wandering albatross
western gull 1
western gull 2
wood duck
Species
0
5
10
15
Mean AFR (years)


alpine swift
black−browed albatross
blue−footed booby
blue tit 1
blue tit 2
common buzzard
Eurasian oystercatcher
Florida scrub−jay
great tit
green woodhoopoe
grey−headed albatross
house sparrow
long−tailed tit
merlin
mute swan
pinyon jay
short−tailed shearwater
Siberian jay
ural owl
wandering albatross
western gull 2
wood duck
Age at first reprodcution (years)
Mean Lifespan (years)
Sex
Both sexes
Female
Male
0
5
10
15
20
25


alpine swift
azure−winged magpie
barn swallow
black−browed albatross
blue−footed booby
blue tit 1
blue tit 2
collared flycatcher
common barn owl
common buzzard
Eurasian oystercatcher
Eurasian sparrowhawk
Florida scrub−jay
goshawk
great tit
green woodhoopoe
grey−headed albatross
house sparrow
indigo bunting
lesser snow goose
long−tailed tit
meadow pipit
merlin
mute swan
osprey
pied flycatcher
pinyon jay
Seychelles warbler
short−tailed shearwater
Siberian jay
tawny owl
ural owl
wandering albatross
western gull 1
western gull 2
wood duck
Lifetime reproductive success (standirdized)
Age at first reproduction (years)
Sex
Both sexes
Female
Male


Optimal AFR
Age at maturity
Mean Lifespan
Age (years)
Mean lifespan (years)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
Barn Swallow
Blue Tit 2
Blue Tit 1
Meadow Pipit
Long-tailed Tit
Great Tit
House Sparrow
Common Barn Owl
Collared Flycatcher
Merlin
Pied Flycatcher
Wood Duck
Azure-winged Magpie
Eurasian Sparrowhawk
Siberian Jay
Seychelles Warbler
Florida Scrub-Jay
Pinyon Jay
Common Buzzard
Tawny Owl
Indigo Bunting
Lesser Snow Goose
Alpine Swift
Green Woodhoopoe
Goshawk
Osprey
Ural Owl
Mute Swan
Short-tailed Shearwater
Western Gull 1
Western Gull 2
Blue-footed Booby
Eurasian Oystercatcher
Black-browed Albatross
Wandering Albatross
Grey-headed Albatross

SUPPORTING INFORMATION

Lifespan and reproductive cost explain interspecific variation in the optimal onset of reproduction

Authors

Emeline Mourocq,[1*] Pierre Bize,[2] Sandra Bouwhuis,[3,4] Russell Bradley,[5] Anne Charmantier,[6] Carlos de la Cruz,[7] Szymon M. Drobniak,[1] Richard H. M. Espie,[8] Márton Herényi,[9,10] Hermann Hötker,[11] Oliver Krüger,[12] John Marzluff,[13] Anders P. Møller,[14] Shinichi Nakagawa,[15,16] Richard A. Phillips,[17] Andrew N. Radford,[18] Alexandre Roulin,[19] János Török,[9] Juliana Valencia,[20] Martijn van de Pol,[21,22] Ian G. Warkentin,[23] Isabel S. Winney,[24] Andrew G. Wood,[17] Michael Griesser[1]

Author affiliation

[1] *University of Zurich, Anthropological Institute & Museum, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland*

[2] *University of Aberdeen, Institute of Biological & Environmental Sciences, Zoology Building, Tillydrone Avenue, Aberdeen AB24 2TZ, United Kingdom*

[3] *Institute of Avian Research "Vogelwarte Helgoland", An der Vogelwarte 21, D-26386 Wilhelmshaven, Germany*

[4] *University of Oxford, Edward Grey Institute, Department of Zoology, Tinbergen Building, South Parks Road, Oxford, OX1 3PS, United Kingdom*

[5] *Point Blue Conservation Science, 3820 Cypress Drive #11, Petaluma 94954, California, United States of America*

[6] *Centre d'Ecologie Fonctionnelle et Evolutive, CNRS UMR 5175, 1919, route de Mende, F-34293 Montpellier, France*

[7] *University of Extremadura, Biology & Ethology Research Group, Avenida de Elvas, E-06071 Badajoz, Spain*

[8] *Technical Resource Branch, Saskatchewan Environment, 5th Floor, 3211 Albert Street, Regina, Saskatchewan S4S 5W6, Canada*

[9] *Eötvös Loránd University, Department of Systematic Zoology & Ecology, Behavioral Ecology Group, Pázmány Péter sétány 1/c., H-1117 Budapest, Hungary*

[10] *Szent István University, Department of Zoology and Animal Ecology, Páter Károly utca 1., H-2100 Gödöllő, Hungary*

[11] *Michael-Otto-Institute within NABU, Goosstroot 1, D-24861Bergenhusen, Germany*

[12] *Bielefeld University, Department of Animal Behavior, Morgenbreede 45, D-33615 Bielefeld, Germany*

[13] *University of Washington, College of The Environment, School of Environmental and Forest Sciences, 4000 15th Avenue NE, Seattle WA 98195-2100, United States of America*

[14] *Université Paris-Sud, Laboratoire d'Ecologie, Systématique & Evolution, CNRS UMR 8079, 362 Rue du Doyen André Guinier, F-91405 Orsay, France*

[15] *University of Otago, Department of Zoology, 340 Great King Street, PO Box 56, Dunedin 9054, New Zealand*

[16] *Evolution & Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia*

[17] *British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, United Kingdom*

[18] *University of Bristol, School of Biological Sciences, 24 Tyndall Avenue, Bristol BS8 1TH, United Kingdom*

[19] *University of Lausanne, Department of Ecology & Evolution, CH-1015 Lausanne, Switzerland*

[20] *University of Córdoba, Department of Zoology, Cátedra Recursos Cinegéticos, Campus de Rabanales, E-14071 Córdoba, Spain*

[21] *Australian National University, Evolution, Ecology & Genetics, Acton ACT 2601, Australia*

[22] *Netherlands Institute of Ecology (NIOO-KNAW), Department of Animal Ecology, Droevendaalsesteeg 10, NL-6708 PB Wageningen, the Netherlands*

[23] *Memorial University of Newfoundland, Environmental Science Program, Corner Brook, NL A2H 6P9, Canada*

[24] *University of Sheffield, Department of Animal & Plant Sciences, Western Bank, Sheffield S10 2TN, United Kingdom*

Table of Contents

Table S1. Information on the source and the type of LRS data for each study.

Species	Scientific name	Location	LRS type	Sample size*	Reference
alpine swift	*Apus melba*	North-Western Switzerland	fledglings	F: 157; M: 121	**Pierre Bize**
azure-winged magpie	*Cyanopica cyanus*	Valdesequera, Spain	fledglings	F: 200; M: 104	**Juliana Valencia & Carlos de la Cruz**
barn swallow	*Hirundo rustica*	Kraghede, Denmark	fledglings	F: 1394; M: 1360	**Anders Pape Møller**
black-browed albatross	*Thalassarche melanophris*	Bird Island, UK	fledglings	B: 76	**Richard Phillips & Andrew G. Wood**
blue Tit 1	*Cyanistes caeruleus*	Oxford, UK	recruits	F: 1177; M: 972	**Sandra Bouwhuis & Ben Sheldon**
blue Tit 2	*Cyanistes caeruleus*	Vienna, Austria	recruits	F: 261; M: 211	**Bart Kempenaers & Emmi Schlicht**
blue-footed booby	*Sula nebouxii*	Isla Isabela, Mexico	fledglings	F: 222; M: 246	Kim et al. (2011)
collared flycatcher	*Ficedula albicollis*	Budapest, Hungary	recruits	F: 453; M: 481	**Márton Herényi & János Török**
common barn owl	*Tyto alba*	Payerne, Switzerland	fledglings	F: 170; M: 174	**Alexandre Roulin**
common buzzard	*Buteo buteo*	Eastern Westphalia, Germany	fledglings	F: 239	**Olivier Krüger**
Eurasian sparrowhawk	*Accipiter nisus*	Annandale, Eskdale, Scotland	fledglings	F: 52	McGraw & Caswell (1996)
Eurasian oystercatcher	*Haematopus ostralegus*	Schiermonnikoog, Netherlands	fledglings	F: 19; M: 33	**Martijn Van de Pol**
Florida scrub-jay	*Aphelocoma coerulescens*	Archbold, USA	fledglings	F: 37; M: 43	Fitzpatrick & Woolfenden (1988)
goshawk	*Accipiter gentilis*	Bissendorf, Spenge, Germany	fledglings	F: 74	Krüger (2005)
great tit	*Parus major*	Oxford, UK	recruits	F: 4935; M: 4370	**Sandra Bouwhuis & Ben Sheldon**
green woodhoopoe	*Phoeniculus purpureus*	Eastern Cape, South Africa	fledglings	F: 59; M: 62	**Andrew Radford**
grey-headed albatross	*Thalassarche chrysostoma*	Bird Island, UK	fledglings	B: 74	**Richard Phillips & Andrew G. Wood**
house sparrow	*Passer domesticus*	Lundy Island, UK	fledglings	F: 287; M: 265	**Terry Burke & colleagues**
indigo bunting	*Passerina cyanea*	Southern Michigan, USA	fledglings	F: 360; M: 357	Payne (1989)
lesser snow goose	*Chen caerulescens*	La Perouse Bay, Canada	1st 4 years of life	F: 2616	Viallefont et al. (1995)
long-tailed tit	*Aegithalos caudatus*	Sheffield, UK	recruits	F: 119; M: 109	**Ben Hatchwell**
meadow pipit	*Anthus pratensis*	North-west Germany	fledglings	F: 33; M: 49	**Hermann Hötker**
merlin	*Falco columbarius*	Saskatoon, Canada	fledglings	F: 26; M: 68	**Richard Espie & Ian G. Warkentin**
mute swan	*Cygnus olor*	Abbotsbury, UK	recruits	F: 252; M: 277	**Anne Charmantier, Ben Sheldon & Chris Perrins**
osprey	*Pandion haliaetus*	Michigan, USA	fledglings	B: 40	Postupalsky (1989)
pied flycatcher	*Ficedula hypoleuca*	Wolfsburg, Germany	fledglings	F: 1411; M: 1135	Sternberg (1989)
pinyon jay	*Gymnorhinus cyanocephalus*	Flagstaff, USA	yearlings	F: 39; M: 41	**John Marzluff**
Seychelles warbler	*Acrocephalus sechellensis*	Cousin Island, Seychelles	fledglings	F: 41; M: 37	Komdeur (1996)
short-tailed shearwater	*Puffinus tenuirostris*	Fisher Island, Australia	fledglings	B: 186	Wooller et al. (1989)
Siberian jay	*Perisoreus infaustus*	Arvidsjaur, Sweden	fledglings	F: 44; M: 56	Ekman & Griesser (2016)
tawny owl	*Strix aluco*	Kielder Forest, UK	fledglings	F: 83; M: 51	Millon et al. (2010)
ural owl	*Strix uralensis*	Päijät-Häme, Finland	fledglings	F: 57	Brommer et al. (1998)
wandering albatross	*Diomedea exulans*	Bird Island, UK	fledglings	F: 1819; M: 1519	**Richard Phillips & Andrew G. Wood**
western gull 1	*Larus occidentalis*	Farallon Island, USA	fledglings	F: 163; M: 108	Pyle et al. (1997)
western gull 2	*Larus occidentalis*	Farallon Island, USA	fledglings	F: 66; M: 93	**Russell Bradley**
wood duck	*Aix sponsa*	South Carolina, USA	fledglings	F: 90	Oli et al. (2002)

Bold reference indicates unpublished data provided directly by researchers.* number of individuals of F: female, M: male, B: both sexes

Table S2. Model without weighting (see Table 2 for output model with weighting) - Effect of sex, mean lifespan of species, family-living and presence of helpers on mean AFR within a species (N = 26 populations, 24 species for which data were available for both sexes). Estimates and 95% confidence intervals (CI) are presented. Δ AICc corresponds to the change in AICc when the specific parameter was included vs. excluded from the full model.

	Standard deviation	Estimate	95% CI	Δ AIC_c
Fixed effects:				
intercept		0.10	(-0.14, 0.34)	-
sex: Females		0.00	na	1.99
sex: Male		0.02	(-0.03, 0.07)	
mean lifespan $_{species}$*		0.82	(0.67, 0.96)	-58.68†
family-living: NO		0.00	na	2.60
family-living: YES		-0.11	(-0.87, 0.66)	
helper presence: NO		0.00	na	2.07
helper presence: YES		-0.34	(-1.18, 0.50)	
Random effects:				
species	0.52		(0.40, 0.70)	
residuals	0.09		(0.07, 0.12)	

* factor centered and scaled; na – not applicable; † support for inclusion of the factor

Table S3. **Model without weighting** (see Table S11 for output model with weighting). Results from models testing the within- and among-species effect of AFR on LRS (N = 36 populations, 34 species). Estimates and 95% confidence intervals (CI) are presented. Δ AICc corresponds to the change in AICc when the specific parameter was included vs. excluded from the full model.

	Standard deviation	Estimate	95% CI	Δ AIC_c
Fixed effects:				
intercept		0.00	(-0.36, 0.37)	-
ln(body mass)*		-0.01	(-0.17, 0.14)	2.10
sex: Both		0.00	na	3.76
sex: Female		0.12	(-0.28, 0.54)	
sex: Male		0.14	(-0.26, 0.54)	
within-species AFR*		-0.38	(-0.56, -0.20)	-14.97†
within-species AFR^2*		-0.30	(-0.51, -0.10)	-6.36†
between-species AFR		0.03	(-0.16, 0.22)	2.03
Random effects:				
species	0.00		(0.00, 0.13)	
residuals	0.86		(0.79, 0.93)	

* factor centered and scaled; na – not applicable; † support for inclusion of the factor

Table S4. Model without weighting (see Table 3 for output model with weighting). Relative importance of predictors included in the full model for the analysis of Delay Index variation excluding Lifespan Effect Index (N = 36 populations, 34 species) and model averaging estimates (based on 58 models with Δ AICc ($AICc_{focal\ model}$ – $AICc_{best\ model}$) ≤ 5, see Table S6).

Predictors	**Predictor weight***	**Relative importance of predictors†**	**Model averaging estimates‡,§**	**95% CI**
intercept			0.07	(-0.78, 0.92)
ln(body mass)	0.49	1.00	0.36	(0.08, 0.64)
sex	0.49	1.00	Both: 0.00 Female: -0.01 Male: -0.05	na (-0.92, 0.89) (-0.97, 0.87)
Choice Index ¶	0.49	1.00	0.59	(0.34, 0.85)
Before Variation Index ¶	0.48	0.98	0.30	(0.08, 0.52)
Before Variation Index: Choice Index	0.34	0.70	0.25	(0.01, 0.71)
latitude	0.17	0.35	-0.06	(-0.42, 0.06)
After Variation Index ¶	0.12	0.25	-0.03	(-0.31, 0.09)
mean lifespan	0.10	0.20	0.04	(-0.16, 0.54)
family-living	0.08	0.16	NO: 0.00 YES: -0.03	na (-0.65, 0.31)
nest predation risk	0.07	0.14	0.01	(-0.20, 0.31)
helper presence	0.06	0.12	NO: 0.00 YES: -0.00	na (-0.69, 0.66)
chick development mode	0.05	0.11	Altricial: 0.00 Precocial: 0.00	na (-0.75, 0.76)
Choice Index: family-living	0.01	0.03	NO: 0.00 YES: 0.02	na (-0.42, 1.38)
After Variation Index: Choice Index	0.01	0.02	0.00	(-0.15, 0.34)
Before Variation Index: After Variation Index	0.01	0.02	-0.00	(-0.17, 0.11)
mean lifespan: helper presence	0.00	0.01	0.01	(-0.26, 2.12)
Choice Index: helper presence	0.00	0.01	NO: 0.00 YES: -0.01	na (-1.99, -0.14)

*: sum of model weights from Table S6 including the focal predictor. na – not applicable.

†: predictor weight relative to the highest weighted predictor.

‡: model averaging estimates according to full model averaging approach since the best AIC_c model is not strongly weighted (weight = 0.04) (Symonds and Moussalli 2011).

§: reference levels of categorical variables have an estimate of 0; estimates reflect difference in slope between the reference level and focal level.

Note: The relative importance of body mass and sex is due to their inclusion by default in each model to control for allometry and sex differences. All continuous variables are centered and scaled.

¶: predictors reflecting the relationship between LRS and AFR, see Table 1 and the Indices and estimates section of Materials and methods.

Table S5. Model without weighting (see Table 4 for output model with weighting). Relative importance of predictors included in the full model for the analysis of Delay Index variation including Lifespan Effect Index (N = 22 populations, 21 species) and model averaging estimates (based on 28 models with Δ AICc ($AICc_{focal\ model}$ – $AICc_{best\ model}$) ≤ 5, see Table S7).

Predictors	**Predictor weight***	**Relative importance of predictors†**	**Model averaging estimates‡,§**	**95% CI**
intercept			0.16	(-0.67, 0.99)
ln(body mass)	0.51	1.00	0.24	(-0.44, 0.92)
sex	0.51	1.00	Both: 0.00	na
			Female: -0.26	(-1.17, 0.65)
			Male: -0.03	(-0.92, 0.87)
Lifespan Effect Index ¶	0.51	1.00	0.54	(0.32, 0.77)
Choice Index ¶	0.49	0.96	0.32	(0.07, 0.60)
mean lifespan	0.30	0.59	0.33	(0.02, 0.10)
After Variation Index ¶	0.25	0.48	-0.13	(-0.51, -0.03)
helper presence	0.24	0.47	NO: 0.00	na
			YES: 0.47	(-0.10, 2.06)
family-living	0.18	0.35	NO: 0.00	na
			YES: -0.26	(-1.57, 0.08)
latitude	0.08	0.15	-0.04	(-0.60, 0.06)
mean lifespan: helper presence	0.05	0.10	0.15	(0.21, 2.82)
Choice Index: family-living	0.05	0.09	NO: 0.00	na
			YES: 0.04	(-0.01, 0.95)
Choice Index: helper presence	0.04	0.08	NO: 0.00	na
			YES: 0.04	(-0.04, 1.04)
Before Variation Index ¶	0.03	0.05	0.01	(-0.16, 0.34)
chick development mode	0.03	0.05	Altricial: 0.00	na
			Precocial: -0.02	(-1.00, 0.22)
nest predation risk	0.02	0.03	0.00	(-0.32, 0.34)

*: sum of model weights from Table S7 including the focal predictor. na – not applicable.

†: predictor weight relative to the highest weighted predictor.

‡: model averaging estimates according to full model averaging approach since the best AIC_c model is not strongly weighted (weight = 0.08) (Symonds and Moussalli 2011).

§: reference levels of categorical variables have an estimate of 0; estimates reflect difference in slope between the reference level and focal level.

Note: The relative importance of body mass and sex is due to their inclusion by default in each model to control for allometry and sex differences. All continuous variables are centered and scaled.

¶: predictors reflecting the relationship between LRS or survival and AFR, see Table 1 and the Indices and estimates section of Materials and methods.

Table S6. Model without weighting (see Table S9 for output model with weighting). Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index (following on the next page).

	Covariate		**Ecological factors**		**Social lifestyle factors**		**Life-history factors**		**Indices reflecting change in LRS with AFR**			**Interactions**									**Model information**				
(Intercept)	**ln(body mass)**	**sex**	**latitude**	**nest predation risk**	**family-living**	**helper presence**	**mean lifespan**	**chick development mode**	**Choice Index**	**Before Variation Index**	**After Variation Index**	**After Variation Index : Before Variation Index**	**After Variation Index : Choice Index**	**Before Variation Index : Choice Index**	**Choice Index : helper presence**	**Choice Index : family-living**	**mean lifespan : helper presence**	**mean lifespan : family-living**	**nest predation risk : helper presence**	**nest predation risk : family-living**	**df**	**log Likelihood**	**AICc**	**Δ AICc**	**weight**
0.20	0.42	+	-	-	-	-	-	-	0.63	0.30	-	-	-	0.34	-	-	-	-	-	-	9	-68.56	158.58	0.00	0.04
-0.06	0.37	+	-0.17	-	-	-	-	-	0.64	0.34	-	-	-	0.35	-	-	-	-	-	-	10	-67.44	159.19	0.61	0.03
0.14	0.40	+	-	-	-	-	-	-	0.50	0.23	-	-	-	-	-	-	-	-	-	-	8	-70.52	159.75	1.17	0.02
0.05	0.28	+	-	-	-	-	0.20	-	0.65	0.31	-	-	-	0.34	-	-	-	-	-	-	10	-67.80	159.91	1.33	0.02
0.25	0.40	+	-	-	-	-	-	-	0.62	0.31	-0.10	-	-	0.35	-	-	-	-	-	-	10	-68.07	160.45	1.87	0.02
-0.12	0.35	+	-0.17	-	-	-	-	-	0.51	0.27	-	-	-	-	-	-	-	-	-	-	9	-69.52	160.49	1.92	0.02
0.19	0.35	+	-	0.12	-	-	-	-	0.64	0.32	-	-	-	0.41	-	-	-	-	-	-	10	-68.10	160.52	1.94	0.02
-0.03	0.34	+	-0.19	-	-	-	-	-	0.63	0.35	-0.11	-	-	0.36	-	-	-	-	-	-	11	-66.71	160.70	2.12	0.01
0.20	0.42	+	-	-	+	-	-	-	0.62	0.29	-	-	-	0.35	-	-	-	-	-	-	10	-68.29	160.90	2.32	0.01
-0.02	0.25	+	-	-	-	-	0.20	-	0.52	0.25	-	-	-	-	-	-	-	-	-	-	9	-69.77	161.00	2.42	0.01
-0.09	0.37	+	-0.19	-	+	-	-	-	0.63	0.33	-	-	-	0.36	-	-	-	-	-	-	11	-66.94	161.15	2.57	0.01
0.08	0.22	+	-	-	-	-	0.24	-	0.64	0.33	-0.12	-	-	0.35	-	-	-	-	-	-	11	-67.00	161.29	2.71	0.01
0.22	0.41	+	-	-	-	-	-	+	0.63	0.30	-	-	-	0.36	-	-	-	-	-	-	10	-68.54	161.39	2.81	0.01
0.20	0.42	+	-	-	-	+	-	-	0.63	0.30	-	-	-	0.34	-	-	-	-	-	-	10	-68.56	161.43	2.85	0.01
-0.10	0.34	+	-0.21	-	-	+	-	-	0.63	0.33	-	-	-	0.35	-	-	-	-	-	-	11	-67.18	161.64	3.07	0.01
-0.03	0.32	+	-0.19	-	-	-	-	+	0.66	0.34	-	-	-	0.41	-	-	-	-	-	-	11	-67.21	161.70	3.12	0.01
-0.04	0.33	+	-0.15	0.08	-	-	-	-	0.64	0.35	-	-	-	0.39	-	-	-	-	-	-	11	-67.25	161.78	3.20	0.01
0.25	0.29	+	-	0.16	-	-	-	-	0.64	0.35	-0.13	-	-	0.44	-	-	-	-	-	-	11	-67.25	161.78	3.20	0.01
0.17	0.38	+	-	-	-	-	-	-	0.50	0.24	-0.08	-	-	-	-	-	-	-	-	-	9	-70.17	161.81	3.23	0.01
-0.08	0.31	+	-0.13	-	-	-	0.10	-	0.64	0.33	-	-	-	0.35	-	-	-	-	-	-	11	-67.29	161.86	3.28	0.01
-0.01	0.48	+	-	-	-	-	-	-	0.49	-	-	-	-	-	-	-	-	-	-	-	7	-72.98	162.03	3.45	0.01
0.09	0.44	+	-	-	-	-	-	+	0.50	0.24	-	-	-	-	-	-	-	-	-	-	9	-70.30	162.05	3.47	0.01
0.18	0.43	+	-	-	+	-	-	-	0.54	0.28	-	-	-	0.34	-	+	-	-	-	-	11	-67.39	162.06	3.48	0.01
0.13	0.40	+	-	-	+	-	-	-	0.50	0.23	-	-	-	-	-	-	-	-	-	-	9	-70.34	162.15	3.57	0.01

Table S6 following. Model without weighting (see Table S9 for output model with weighting). Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index (following on the next page).

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS with AFR			Interactions									Model information				
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	After Variation Index : Before Variation Index	After Variation Index : Choice Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likihood	AICc	Δ AICc	weight
-0.10	0.32	+	-0.18	-	-	-	-	-	0.50	0.28	-0.10	-	-	-	-	-	-	-	-	-	10	-68.99	162.29	3.71	0.01
0.13	0.39	+	-	0.02	-	-	-	-	0.50	0.24	-	-	-	-	-	-	-	-	-	-	9	-70.50	162.47	3.89	0.01
0.13	0.40	+	-	-	-	+	-	-	0.50	0.23	-	-	-	-	-	-	-	-	-	-	9	-70.51	162.49	3.91	0.01
0.06	0.29	+	-	-	+	-	0.18	-	0.64	0.30	-	-	-	0.35	-	-	-	-	-	-	11	-67.64	162.56	3.98	0.01
-0.15	0.35	+	-0.18	-	+	-	-	-	0.50	0.26	-	-	-	-	-	-	-	-	-	-	10	-69.16	162.64	4.06	0.01
0.01	0.20	+	-	-	-	-	0.24	-	0.52	0.26	-0.11	-	-	-	-	-	-	-	-	-	10	-69.17	162.66	4.08	0.01
-0.06	0.34	+	-0.21	-	+	-	-	-	0.63	0.35	-0.11	-	-	0.37	-	-	-	-	-	-	12	-66.20	162.77	4.19	0.01
0.08	0.28	+	-	0.05	-	-	0.16	-	0.65	0.32	-	-	-	0.37	-	-	-	-	-	-	11	-67.75	162.77	4.20	0.01
-0.08	0.29	+	-0.24	-	-	+	-	-	0.63	0.35	-0.13	-	-	0.37	-	-	-	-	-	-	12	-66.23	162.82	4.24	0.01
0.26	0.40	+	-	-	-	-	-	-	0.62	0.31	-0.12	-	0.10	0.39	-	-	-	-	-	-	11	-67.77	162.83	4.25	0.01
0.06	0.27	+	-	-	-	+	0.20	-	0.65	0.31	-	-	-	0.34	-	-	-	-	-	-	11	-67.79	162.87	4.29	0.00
0.05	0.28	+	-	-	-	-	0.20	+	0.65	0.31	-	-	-	0.34	-	-	-	-	-	-	11	-67.80	162.87	4.29	0.00
0.01	0.27	+	-0.16	0.12	-	-	-	-	0.64	0.38	-0.14	-	-	0.43	-	-	-	-	-	-	12	-66.25	162.88	4.30	0.00
0.24	0.40	+	-	-	+	-	-	-	0.62	0.30	-0.09	-	-	0.36	-	-	-	-	-	-	11	-67.82	162.91	4.33	0.00
0.16	0.46	+	-	-	+	+	-	-	0.62	0.30	-	-	-	0.35	-	-	-	-	-	-	11	-67.85	162.98	4.40	0.00
-0.15	0.33	+	-0.20	-	-	+	-	-	0.51	0.27	-	-	-	-	-	-	-	-	-	-	10	-69.34	162.99	4.41	0.00
-0.14	0.28	+	-0.13	-	-	-	0.11	-	0.52	0.27	-	-	-	-	-	-	-	-	-	-	10	-69.35	163.01	4.43	0.00
0.19	0.36	+	-	0.11	+	-	-	-	0.64	0.32	-	-	-	0.41	-	-	-	-	-	-	11	-67.87	163.01	4.44	0.00
-0.10	0.29	+	-	-	-	-	0.22	+	0.52	0.26	-	-	-	-	-	-	-	-	-	-	10	-69.39	163.08	4.51	0.00
0.11	0.41	+	-	-	+	-	-	-	0.41	0.21	-	-	-	-	-	+	-	-	-	-	10	-69.39	163.09	4.51	0.00
-0.13	0.37	+	-0.16	-	-	-	-	+	0.51	0.27	-	-	-	-	-	-	-	-	-	-	10	-69.46	163.24	4.66	0.00
-0.05	0.25	+	-0.14	-	-	-	0.14	-	0.64	0.35	-0.12	-	-	0.36	-	-	-	-	-	-	12	-66.44	163.25	4.67	0.00
0.25	0.40	+	-	-	-	-	-	-	0.63	0.33	-0.09	-0.03	-	0.35	-	-	-	-	-	-	11	-67.98	163.25	4.67	0.00
-0.01	0.35	+	-0.19	-	-	-	-	-	0.63	0.35	-0.14	-	0.09	0.39	-	-	-	-	-	-	12	-66.44	163.25	4.67	0.00

Table S6 following. Model without weighting (see Table S9 for output model with weighting). Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index (following on the next page).

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS with AFR			Interactions									Model information				
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	After Variation Index : Before Variation Index	After Variation Index : Choice Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likihood	AICc	Δ AICc	weight
-0.12	0.36	+	-0.17	-0.02	-	-	-	-	0.51	0.27	-	-	-	-	-	-	-	-	-	-	10	-69.50	163.32	4.74	0.00
0.25	0.39	+	-	-	-	+	-	-	0.62	0.31	-0.10	-	-	0.36	-	-	-	-	-	-	11	-68.06	163.40	4.82	0.00
0.26	0.39	+	-	-	-	-	-	+	0.63	0.31	-0.09	-	-	0.36	-	-	-	-	-	-	11	-68.06	163.41	4.83	0.00
0.00	0.29	+	-0.21	-	-	-	-	+	0.65	0.36	-0.11	-	-	0.41	-	-	-	-	-	-	12	-66.53	163.43	4.85	0.00
0.18	0.36	+	-	0.13	-	-	-	+	0.64	0.33	-	-	-	0.40	-	-	-	-	-	-	11	-68.09	163.46	4.88	0.00
0.19	0.35	+	-	0.12	-	+	-	-	0.64	0.33	-	-	-	0.41	-	-	-	-	-	-	11	-68.10	163.48	4.90	0.00
-0.03	0.34	+	-0.19	-	-	-	-	-	0.64	0.37	-0.10	-0.04	-	0.36	-	-	-	-	-	-	12	-66.57	163.50	4.92	0.00
0.11	0.28	+	-	-	-	+	0.16	-	0.60	0.29	-	-	-	0.33	-	-	+	-	-	-	12	-66.58	163.52	4.94	0.00
-0.04	0.26	+	-	-0.08	-	-	0.26	-	0.53	0.24	-	-	-	-	-	-	-	-	-	-	10	-69.61	163.53	4.95	0.00
0.02	0.48	+	-	-	+	+	-	-	0.42	0.20	-	-	-	-	+	+	-	-	-	-	12	-66.59	163.54	4.96	0.00

Model set with Δ AICc ≤ 5. N = 36 populations, 34 species.

"+" and "-" indicate the presence or absence of the parameter in the model, respectively. "df" is the degree of freedom. "log Likelihood" is the log likelihood of the model. "AIC_c" represents the Akaike's information criterion corrected for sample size. "Δ AIC_c" is the difference in AIC_c between the focal model and the model with the lowest AIC_c. "weight" represents the relative probability of a model within the full set of models.

Table S7. Model without weighting (see Table S10 for output model with weighting). Model selection output for the analysis of Delay Index variation including Lifespan Effect Index (following on the next page).

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS or survival with AFR				Interactions						Model information				
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	Lifespan Effect Index	Before Variation Index : Choice	Choice Index : helper presence	Choice Index : family-living	mean lifespan: helper presence	mean lifespan: family-living	nest predation risk : family-living	df	logLikelihood	AICc	Δ AICc	weight
0.11	-0.07	+	-	-	-	-	0.66	-	0.36	-	-0.27	0.54	-	-	-	-	-	-	10	-30.40	89.61	0.00	0.08
0.31	0.65	+	-	-	+	+	-	-	0.35	-	-	0.57	-	-	-	-	-	-	10	-31.00	90.79	1.19	0.05
0.31	0.60	+	-	-	+	+	-	-	0.20	-	-	0.52	-	-	+	-	-	-	11	-29.15	91.29	1.69	0.04
0.08	0.17	+	-	-	-	-	0.47	-	0.40	-	-	0.56	-	-	-	-	-	-	9	-33.33	91.59	1.99	0.03
0.36	0.56	+	-	-	+	+	-	-	0.22	-	-	0.57	-	+	-	-	-	-	11	-29.38	91.76	2.15	0.03
-0.08	0.43	+	-0.31	-	-	-	-	-	0.40	-	-	0.54	-	-	-	-	-	-	9	-33.56	92.04	2.44	0.02
0.03	-0.03	+	-	-	-	-	0.70	+	0.36	-	-0.33	0.52	-	-	-	-	-	-	11	-29.56	92.12	2.52	0.02
-0.12	-0.03	+	-0.19	-	-	-	0.54	-	0.37	-	-0.27	0.53	-	-	-	-	-	-	11	-29.58	92.16	2.56	0.02
0.18	-0.06	+	-	-	-	+	0.59	-	0.28	-	-0.28	0.51	-	-	-	+	-	-	12	-27.39	92.36	2.75	0.02
0.09	0.01	+	-	-	-	+	0.62	-	0.39	-	-0.27	0.52	-	-	-	-	-	-	11	-29.71	92.41	2.81	0.02
0.45	0.52	+	-	-	-	-	-	-	0.38	-	-	0.56	-	-	-	-	-	-	8	-35.72	92.77	3.16	0.02
0.15	-0.12	+	-	-	-	+	0.64	-	0.25	-	-0.30	0.53	-	+	-	-	-	-	12	-27.68	92.92	3.31	0.02
-0.01	0.36	+	-0.33	-	-	-	-	-	0.37	-	-0.17	0.53	-	-	-	-	-	-	10	-32.30	93.39	3.79	0.01
0.09	-0.09	+	-	-	+	-	0.69	-	0.38	-	-0.29	0.53	-	-	-	-	-	-	11	-30.33	93.65	4.05	0.01
-0.18	0.21	+	-0.21	-	-	-	0.34	-	0.40	-	-	0.54	-	-	-	-	-	-	10	-32.46	93.73	4.12	0.01
0.35	0.42	+	-	-	+	+	0.04	-	-	-	-	0.57	-	-	-	+	-	-	11	-30.36	93.73	4.12	0.01
0.10	-0.08	+	-	0.05	-	-	0.64	-	0.37	-	-0.27	0.56	-	-	-	-	-	-	11	-30.37	93.75	4.14	0.01
0.11	-0.07	+	-	-	-	-	0.66	-	0.36	0.02	-0.27	0.54	-	-	-	-	-	-	11	-30.39	93.77	4.16	0.01
0.34	0.63	+	-	-	+	+	-	-	0.36	0.12	-	0.52	-	-	-	-	-	-	11	-30.43	93.86	4.25	0.01
0.25	-0.19	+	-	-	-	+	0.58	-	-	-	-0.32	0.53	-	-	-	+	-	-	11	-30.46	93.92	4.32	0.01
0.26	0.44	+	-	-	+	+	0.14	-	0.25	-	-	0.55	-	-	-	+	-	-	12	-28.19	93.95	4.34	0.01
0.42	0.46	+	-	-	+	-	-	-	0.14	-	-	0.52	-	-	+	-	-	-	10	-32.59	93.97	4.36	0.01
0.06	0.25	+	-	-	-	+	0.43	-	0.43	-	-	0.53	-	-	-	-	-	-	10	-32.63	94.06	4.45	0.01
0.17	0.48	+	-	-	+	+	0.21	-	0.37	-	-	0.56	-	-	-	-	-	-	11	-30.55	94.09	4.49	0.01

Table S7 following. Model without weighting (see Table S10 for output model with weighting). Model selection output for the analysis of Delay Index variation including Lifespan Effect Index (following on the next page).

	Covariate		**Ecological factors**		**Social lifestyle factors**		**Life-history factors**		**Indices reflecting change in LRS or survival with AFR**				**Interactions**						**Model information**				
(Intercept)	**ln(body mass)**	**sex**	**latitude**	**nest predation risk**	**family-living**	**helper presence**	**mean lifespan**	**chick development mode**	**Choice Index**	**Before Variation Index**	**After Variation Index**	**Lifespan Effect Index**	**Before Variation Index : Choice**	**Choice Index : helper presence**	**Choice Index : family-living**	**mean lifespan: helper presence**	**mean lifespan: family-living**	**nest predation risk : family-living**	**df**	**log Likelihood**	**AICc**	**Δ AICc**	**weight**
0.39	0.59	+	-	-	-	+	-	-	0.42	-	-	0.53	-	-	-	-	-	-	9	-34.70	94.33	4.72	0.01
0.25	0.56	+	-	0.13	+	+	-	-	0.37	-	-	0.60	-	-	-	-	-	-	11	-30.73	94.46	4.85	0.01
-0.15	0.37	+	-0.37	-	-	-	-	-	0.42	0.14	-	0.48	-	-	-	-	-	-	10	-32.85	94.50	4.90	0.01
0.37	0.62	+	-	-	+	+	-	-	0.34	-	-0.07	0.56	-	-	-	-	-	-	11	-30.76	94.53	4.92	0.01

Model set with Δ AICc ≤ 5. N = 22 populations, 21 species.

"+" and "-" indicate the presence or absence of the parameter in the model, respectively. "df" is the degree of freedom. "log Likelihood" is the log likelihood of the model. "AIC_c" represents the Akaike's information criterion corrected for sample size. "Δ AIC_c" is the difference in AIC_c between the focal model and the model with the lowest AIC_c. "weight" represents the relative probability of a model within the full set of models.

Table S8. Justification for the interactions used in the analysis of the Delay Index.

Interaction	Reason for inclusion in the model
Before Variation Index *x* After Variation Index	To test if the relative timing of the Optimal AFR over reproductive lifespan (Delay Index) was influenced simultaneously by a LRS cost from initiating reproduction both before the optimal timing (Before Variation Index) and after the optimal timing (After Variation Index).
Choice Index *x* Before Variation Index	To test if Delay Index was influenced simultaneously by the level of probability to adopt an AFR leading to the highest fitness return (i.e. the span of "beneficial AFR" within the observed range of AFR) and a LRS cost from initiating reproduction before Optimal AFR. *We expect species with a large span of "beneficial AFR" and a low LRS cost of early reproduction to benefit from a late AFR.*
Choice Index *x* After Variation Index	To test if Delay Index was influenced simultaneously by the level of probability to adopt an AFR leading to the highest fitness return (i.e. the span of "beneficial AFR" within the observed range of AFR) and a LRS cost from initiating reproduction after Optimal AFR. *We expect species with a small span of "beneficial AFR" and a high LRS cost of late reproduction to benefit from an early AFR.*
Mean lifespan *x* Family-living	For each of these interactions we tested whether sociality influenced the effect of the focal predictors on Delay Index based on the idea that living in a kin group (Family living) or breeding cooperatively (Helper presence) might buffer costs associated with the timing of the AFR within the reproductive lifespan. *For instance, species with a high risk of nest predation need to get experience to successfully defend their nest and have a greater reproductive output. Consequently, they might benefit from a later AFR. However, if the presence of helpers provides anti-predator protection, it might allow less experienced individuals to still achieve a good reproductive output. Therefore, we expect species with a high risk of nest predation breeding cooperatively to benefit more from an earlier AFR than species with a high risk of nest predation but breeding as a pair without helpers.*
Mean lifespan *x* Helper presence	
Nest predation risk *x* Family-living	
Nest predation risk *x* Helper presence	
Choice Index *x* Family-living	
Choice Index *x* Helper presence	

The variables included in the interactions are explained in the manuscript as well as in Table 1 for the indices.

Table S9. Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index (following on the next page).

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS with AFR			Interactions								Model information				
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	After Variation Index : Before Variation Index	After Variation Index : Choice Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.14	0.46	+	-	-	+	+	-	-	0.36	0.22	-	-	-	-	+	+	-	-	-	-	12	-60.84	152.05	0.00	0.05
0.06	0.30	+	-	-0.03	+	+	0.19	-	0.36	0.28	-	-	-	-	-	-	+	+	+	+	16	-54.44	152.97	0.92	0.03
0.06	0.33	+	-	-0.03	+	+	0.17	-	0.37	0.28	-	-	-	-	+	-	+	+	-	+	16	-54.74	153.56	1.51	0.02
0.22	0.47	+	-	-	+	+	-	-	0.47	0.29	-	-	-	0.22	+	+	-	-	-	-	13	-60.14	153.86	1.81	0.02
0.23	0.27	+	-	0.28	-	-	-	-	0.67	0.43	-	-	-	0.52	-	-	-	-	-	-	10	-64.84	153.99	1.94	0.02
0.10	0.22	+	-	-0.04	+	+	0.25	-	0.35	0.30	-0.16	-	-	-	-	-	+	+	+	+	17	-53.12	154.16	2.11	0.02
0.19	0.44	+	-	-	+	+	-	-	0.36	0.22	-0.11	-	-	-	+	+	-	-	-	-	13	-60.30	154.19	2.14	0.02
0.33	0.43	+	-	-	-	-	-	-	0.62	0.39	-	-	-	0.42	-	-	-	-	-	-	9	-66.41	154.29	2.24	0.02
0.10	0.25	+	-	-0.04	+	+	0.24	-	0.37	0.29	-0.17	-	-	-	+	-	+	+	-	+	17	-53.28	154.48	2.43	0.01
0.07	0.36	+	-	-0.02	+	+	0.12	-	0.34	0.27	-	-	-	-	-	-	+	+	-	+	15	-57.10	154.64	2.59	0.01
0.10	0.49	+	-	-	+	+	-	+	0.37	0.23	-	-	-	-	+	+	-	-	-	-	13	-60.60	154.79	2.74	0.01
-0.02	0.40	+	-0.10	-	+	+	-	-	0.38	0.24	-	-	-	-	+	+	-	-	-	-	13	-60.61	154.81	2.76	0.01
0.09	0.50	+	-	-	+	+	-	-	0.35	-	-	-	-	-	+	+	-	-	-	-	11	-63.77	154.82	2.77	0.01
0.08	0.39	+	-	-	+	+	0.09	-	0.37	0.23	-	-	-	-	+	+	-	-	-	-	13	-60.73	155.03	2.98	0.01
0.30	0.22	+	-	0.32	-	-	-	-	0.69	0.46	-0.15	-	-	0.57	-	-	-	-	-	-	11	-63.89	155.06	3.01	0.01
0.06	0.32	+	-	-0.03	+	+	0.17	-	0.37	0.29	-	-	-	-	-	+	+	+	-	+	16	-55.49	155.06	3.01	0.01
0.13	0.45	+	-	0.02	+	+	-	-	0.37	0.22	-	-	-	-	+	+	-	-	-	-	13	-60.83	155.25	3.20	0.01
0.15	0.29	+	-	0.03	+	+	0.14	-	0.46	0.35	-	-	-	0.23	-	-	+	+	+	+	17	-53.73	155.38	3.33	0.01
0.05	0.23	+	-	0.03	+	+	0.22	+	0.36	0.33	-0.22	-	-	-	-	-	+	+	+	+	18	-51.82	155.55	3.50	0.01
0.05	0.28	+	-	-0.03	+	+	0.21	-	0.38	0.29	-	-	-	-	-	+	+	+	+	+	17	-53.84	155.60	3.55	0.01
0.30	0.44	+	-	-	+	+	-	-	0.47	0.31	-0.13	-	-	0.25	+	+	-	-	-	-	14	-59.38	155.69	3.64	0.01
0.10	0.23	+	-	-0.04	+	+	0.25	-	0.37	0.30	-0.17	-	-	-	-	+	+	+	-	+	17	-54.01	155.92	3.87	0.01
0.22	0.20	+	-	0.04	+	+	0.21	-	0.48	0.38	-0.18	-	-	0.28	-	-	+	+	+	+	18	-52.01	155.93	3.88	0.01
0.06	0.30	+	-	-0.03	+	+	0.19	-	0.37	0.28	-	-	-	-	+	-	+	+	+	+	17	-54.04	155.99	3.94	0.01
0.11	0.29	+	-	-0.03	+	+	0.19	-	0.33	0.28	-0.15	-	-	-	-	-	+	+	-	+	16	-55.97	156.03	3.98	0.01

Table S9 following. Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index.

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS with AFR			Interactions									Model information				
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	After Variation Index : Before Variation Index	After Variation Index : Choice Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.02	0.32	+	-	0.01	+	+	0.16	+	0.36	0.30	-	-	-	-	-	-	+	+	+	+	17	-54.06	156.03	3.98	0.01
0.44	0.35	+	-	-	-	-	-	+	0.65	0.40	-	-	-	0.48	-	-	-	-	-	-	10	-65.86	156.04	3.99	0.01
0.15	0.32	+	-	0.03	+	+	0.12	-	0.47	0.35	-	-	-	0.22	+	-	+	+	-	+	17	-54.07	156.05	4.00	0.01
0.10	0.39	+	-	-	+	+	0.07	-	0.37	0.22	-	-	-	-	+	+	+	-	-	-	14	-59.66	156.25	4.20	0.01
0.39	0.42	+	-	-	-	-	-	-	0.63	0.40	-0.11	-	-	0.44	-	-	-	-	-	-	10	-65.98	156.27	4.22	0.01
0.22	0.22	+	-	0.03	+	+	0.19	-	0.49	0.38	-0.19	-	-	0.28	+	-	+	+	-	+	18	-52.21	156.33	4.28	0.01
0.06	0.26	+	-	0.02	+	+	0.21	+	0.37	0.33	-0.22	-	-	-	+	-	+	+	-	+	18	-52.22	156.34	4.29	0.01
0.10	0.39	+	-0.13	-	-	-	-	-	0.63	0.41	-	-	-	0.42	-	-	-	-	-	-	10	-66.04	156.38	4.33	0.01
0.18	0.35	+	-	0.05	+	+	0.07	-	0.46	0.35	-	-	-	0.27	-	-	+	+	-	+	16	-56.16	156.41	4.36	0.01
0.16	0.48	+	-	-	+	+	-	+	0.36	0.24	-0.14	-	-	-	+	+	-	-	-	-	14	-59.74	156.42	4.37	0.01
0.25	0.20	+	-	0.05	+	+	0.20	-	0.53	0.42	-0.20	-	-	0.35	-	+	+	+	-	+	18	-52.32	156.54	4.49	0.01
-0.02	0.34	+	-0.15	-	+	+	-	-	0.38	0.25	-0.14	-	-	-	+	+	-	-	-	-	14	-59.81	156.57	4.52	0.01
0.09	0.20	+	-	-0.04	+	+	0.28	-	0.37	0.31	-0.17	-	-	-	-	+	+	+	+	+	18	-52.33	156.58	4.53	0.00
0.05	0.40	+	-0.11	-	+	+	-	-	0.48	0.31	-	-	-	0.22	+	+	-	-	-	-	14	-59.86	156.66	4.61	0.00
0.18	0.30	+	-	0.05	+	+	0.12	-	0.50	0.38	-	-	-	0.29	-	+	+	+	-	+	17	-54.38	156.67	4.62	0.00
0.30	0.24	+	-	0.25	-	-	-	+	0.68	0.43	-	-	-	0.55	-	-	-	-	-	-	11	-64.70	156.67	4.62	0.00
0.18	0.42	+	-	-	-	-	-	-	0.43	0.25	-	-	-	-	-	-	-	-	-	-	8	-68.98	156.67	4.62	0.00
0.20	0.41	+	-	0.10	+	+	-	-	0.49	0.32	-	-	-	0.27	+	+	-	-	-	-	14	-59.91	156.76	4.71	0.00
0.09	0.30	+	0.03	-0.03	+	+	0.20	-	0.36	0.28	-	-	-	-	-	-	+	+	+	+	17	-54.43	156.76	4.71	0.00
0.30	0.31	+	-	0.32	-	-	-0.09	-	0.66	0.44	-	-	-	0.53	-	-	-	-	-	-	11	-64.74	156.77	4.72	0.00
0.13	0.26	+	-0.06	0.26	-	-	-	-	0.67	0.44	-	-	-	0.52	-	-	-	-	-	-	11	-64.75	156.77	4.72	0.00
0.19	0.44	+	-	-	+	+	-	-	0.36	0.17	-0.14	0.06	-	-	+	+	-	-	-	-	14	-59.94	156.82	4.77	0.00

Table S9 following. Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index.

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS with AFR			Interactions									Model information				
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	After Variation Index : Before Variation Index	After Variation Index : Choice Index	Before Variation Index : Choice Index	Choice Index : helper presence	Choice Index : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.04	0.35	+	-	0.00	+	+	0.15	+	0.37	0.29	-	-	-	-	+	-	+	+	-	+	17	-54.49	156.89	4.84	0.00
0.16	0.38	+	-	-	+	+	0.10	-	0.48	0.30	-	-	-	0.22	+	+	-	-	-	-	14	-59.98	156.90	4.85	0.00
0.25	0.37	+	-	-	-	-	0.09	-	0.63	0.39	-	-	-	0.42	-	-	-	-	-	-	10	-66.30	156.91	4.86	0.00
0.23	0.27	+	-	0.28	-	+	-	-	0.67	0.44	-	-	-	0.52	-	-	-	-	-	-	11	-64.83	156.93	4.88	0.00
0.24	0.27	+	-	0.28	+	-	-	-	0.67	0.44	-	-	-	0.52	-	-	-	-	-	-	11	-64.83	156.95	4.90	0.00
0.11	0.32	+	-	-	+	+	0.14	-	0.37	0.23	-0.13	-	-	-	+	+	-	-	-	-	14	-60.03	157.00	4.95	0.00

Model set with Δ AICc ≤ 5. N = 36 populations, 34 species.

"+" and "-" indicate the presence or absence of the parameter in the model, respectively. "df" is the degree of freedom. "log Likelihood" is the log likelihood of the model. "AIC_c" represents the Akaike's information criterion corrected for sample size. "Δ AIC_c" is the difference in AIC_c between the focal model and the model with the lowest AIC_c. "weight" represents the relative probability of a model within the full set of models.

Table S10. Model selection output for the analysis of Delay Index variation including Lifespan Effect Index.

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS or survival with AFR				Interactions						Model information				
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	Lifespan Effect Index	Before Variation Index : Choice	Choice Index : helper presence	Choice Index : family-living	mean lifespan: helper presence	mean lifespan: family-living	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.36	0.05	+	-	-	-	-	0.53	-	0.36	-	-0.33	0.53	-	-	-	-	-	-	10	-24.97	78.73	0.00	0.10
0.42	0.61	+	-	-	+	+	-	-	0.35	-	-	0.53	-	-	-	-	-	-	10	-25.55	79.90	1.17	0.06
0.35	0.30	+	-	0.39	-	-	-	+	0.38	-	-0.36	0.61	-	-	-	-	-	-	11	-23.91	80.82	2.09	0.04
0.51	0.58	+	-	-	+	+	-	-	0.33	-	-0.19	0.52	-	-	-	-	-	-	11	-23.91	80.82	2.09	0.04
0.35	0.08	+	-	-	-	+	0.53	-	0.38	-	-0.32	0.51	-	-	-	-	-	-	11	-24.30	81.61	2.87	0.02
0.68	0.78	+	0.21	-	+	+	-	-	0.31	-	-	0.54	-	-	-	-	-	-	11	-24.39	81.78	3.05	0.02
0.41	0.16	+	-	-	-	-	0.43	+	0.35	-	-0.36	0.52	-	-	-	-	-	-	11	-24.42	81.85	3.11	0.02
0.28	0.00	+	-	0.18	-	-	0.46	-	0.38	-	-0.33	0.57	-	-	-	-	-	-	11	-24.48	81.97	3.23	0.02
0.60	0.55	+	-	-	-	-	-	+	0.32	-	-0.33	0.54	-	-	-	-	-	-	10	-26.64	82.09	3.36	0.02
0.41	0.59	+	-	-	+	+	-	-	0.31	-	-	0.51	-	-	+	-	-	-	11	-24.69	82.38	3.65	0.02
0.42	0.59	+	-	-	+	+	-	-	0.31	-	-	0.52	-	+	-	-	-	-	11	-24.70	82.41	3.68	0.02
0.29	0.24	+	-	-	-	-	0.37	-	0.38	-	-	0.56	-	-	-	-	-	-	9	-28.90	82.72	3.98	0.01
0.33	-0.01	+	-	-	+	-	0.60	-	0.37	-	-0.35	0.52	-	-	-	-	-	-	11	-24.88	82.76	4.03	0.01
0.33	0.37	+	-0.21	-	-	-	-	-	0.35	-	-0.28	0.55	-	-	-	-	-	-	10	-27.02	82.83	4.10	0.01
0.35	0.04	+	-	-	-	-	0.54	-	0.36	0.02	-0.33	0.52	-	-	-	-	-	-	11	-24.95	82.90	4.17	0.01
0.37	0.04	+	0.02	-	-	-	0.56	-	0.36	-	-0.33	0.53	-	-	-	-	-	-	11	-24.96	82.91	4.18	0.01
0.75	0.80	+	0.28	-	+	+	-	-	0.24	-	-	0.51	-	-	+	-	-	-	12	-22.69	82.94	4.20	0.01
0.41	0.61	+	-	-	+	+	-	-	0.35	0.11	-	0.52	-	-	-	-	-	-	11	-25.04	83.07	4.34	0.01
0.48	0.55	+	-	-	-	-	-	-	0.35	-	-	0.59	-	-	-	-	-	-	8	-30.90	83.14	4.41	0.01
0.33	0.33	+	-	0.40	-	+	-	+	0.41	-	-0.36	0.58	-	-	-	-	-	-	12	-22.80	83.17	4.44	0.01

Table S10 following. Model selection output for the analysis of Delay Index variation including Lifespan Effect Index.

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS or survival with AFR				Interactions						Model information				
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index	Before Variation Index	After Variation Index	Lifespan Effect Index	Before Variation Index : Choice	Choice Index : helper presence	Choice Index : family-living	mean lifespan: helper presence	mean lifespan: family-living	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.50	0.56	+	-	-	+	+	-	-	0.29	-	-0.20	0.50	-	-	+	-	-	-	12	-22.84	83.24	4.51	0.01
0.29	0.26	+	-	0.45	-	-	-	+	0.39	0.17	-0.38	0.59	-	-	-	-	-	-	12	-22.84	83.25	4.52	0.01
0.75	0.78	+	0.27	-	+	+	-	-	0.25	-	-	0.53	-	+	-	-	-	-	12	-22.85	83.26	4.53	0.01
0.51	0.55	+	-	-	+	+	-	-	0.29	-	-0.19	0.52	-	+	-	-	-	-	12	-22.89	83.35	4.62	0.01
0.35	0.27	+	-	0.37	-	-	-	-	0.38	-	-0.24	0.65	-	-	-	-	-	-	10	-27.28	83.37	4.64	0.01
0.52	0.80	+	-	-	+	+	-0.21	-	0.33	-	-	0.54	-	-	-	-	-	-	11	-25.27	83.53	4.80	0.01
0.34	0.53	+	-	0.13	+	+	-	-	0.37	-	-	0.56	-	-	-	-	-	-	11	-25.31	83.61	4.88	0.01
0.58	0.52	+	-	-	-	-	-	-	0.33	-	-0.21	0.58	-	-	-	-	-	-	9	-29.39	83.69	4.96	0.01

Model set with Δ $AIC_c \leq 5$. N = 22 populations, 21 species.

"+" and "-" indicate the presence or absence of the parameter in the model, respectively. "df" is the degree of freedom. "log Likelihood" is the log likelihood of the model. "AIC_c" represents the Akaike's information criterion corrected for sample size. "Δ AIC_c" is the difference in AIC_c between the focal model and the model with the lowest AIC_c. "weight" represents the relative probability of a model within the full set of models.

Table S11. Results from models testing the within- and among-species effect of AFR on LRS (N = 36 populations, 34 species). Estimates and 95% confidence intervals (CI) are presented. Δ AICc corresponds to the change in AICc when the specific parameter was included vs. excluded from the full model.

	Standard deviation	Estimate	95% CI	Δ AIC_c
Fixed effects:				
intercept		-0.12	(-0.87, 0.62)	-
ln(body mass)*		-0.11	(-0.29, 0.08)	0.91
sex: Both		0.00	na	
sex: Female		0.38	(-0.37, 1.14)	3.09
sex: Male		0.41	(-0.34, 1.16)	
within-species AFR*		-0.54	(-0.70, -0.39)	-43.83†
within-species AFR^2*		-0.26	(-0.43, -0.10)	-7.45†
between-species AFR		0.08	(-0.13, 0.29)	1.57
Random effects:				
species	0.00		(0.00, 0.16)	
residuals	19.64		(18.14, 21.35)	

* factor centered and scaled; na – not applicable; † support for inclusion of the factor

Table S12. Correlation between Optimal AFR vs. modal AFR and Optimal AFR vs. mean AFR.

cases	Mean AFR vs. Optimal AFR			AFR mode vs. Optimal AFR		
	Correlation coefficient	P	Slope	Correlation coefficient	P	Slope
all (N=62)	0.84 (Spearman)	< 0.0001	0.95	0.80 (Spearman)	< 0.0001	0.98
with AFR range > 4 (N=29)	0.85 (Spearman)	< 0.0001	0.99	0.87 (Spearman)	< 0.0001	0.82
with AFR range > 6 (N=12)	0.96 (Pearson)	< 0.0001	1.13	0.92 (Pearson)	< 0.0001	1.06

Table S13. Model with 90CI indices (see Table 3 for comparison). Relative importance of predictors included in the full model for the analysis of Delay Index variation excluding Lifespan Effect Index (N = 36 populations, 34 species) and model averaging estimates (based on 51 models with Δ AICc ($AICc_{focal\ model}$ – $AICc_{best\ model}$) ≤ 5, see Table S15).

Predictors	**Predictor weight***	**Relative importance of predictors†**	**Model averaging estimates‡,§**	**95% CI**
intercept			0.42	(-0.60, 1.44)
ln(body mass)	0.51	1.00	0.21	(-0.17, 0.59)
sex	0.51	1.00	Both: 0.00 Female: -0.30 Male: -0.54	na (-1.40, 0.79) (-1.64, 0.56)
Choice Index 90CI ¶	0.51	1.00	0.53	(0.29, 0.77)
Before Variation Index 90CI ¶	0.51	1.00	0.36	(-0.02, 0.74)
Before Variation Index 90CI: Choice Index 90CI	0.51	1.00	0.86	(0.35, 1.37)
nest predation risk	0.41	0.80	0.35	(0.03, 0.84)
After Variation Index 90CI ¶	0.35	0.69	-0.17	(-0.49, 0.01)
Before Variation Index 90CI: After Variation Index 90CI	0.17	0.33	-0.05	(-0.32, 0.01)
family-living	0.13	0.26	NO: 0.00 YES: 0.15	na (-0.95, 2.15)
chick development mode	0.12	0.24	Altricial: 0.00 Precocial: 0.17	na (-0.28, 1.69)
mean lifespan	0.10	0.20	-0.04	(-0.77, 0.35)
helper presence	0.10	0.19	NO: 0.00 YES: -0.12	na (-2.91, 1.63)
nest predation risk: family-living	0.05	0.09	NO: 0.00 YES: 0.09	na (-0.34, 2.21)
Choice Index: helper presence	0.04	0.08	NO: 0.00 YES: -0.12	na (-2.55, -0.30)
latitude	0.04	0.08	0.00	(-0.30, 0.42)
Choice Index: family-living	0.04	0.07	NO: 0.00 YES: 0.11	na (0.62, 2.44)
After Variation Index 90CI: Choice Index 90CI	0.02	0.04	-0.00	(-0.53, 0.48)
mean lifespan: helper presence	0.02	0.03	NO: 0.00 YES: 0.13	na (2.18, 7.04)
mean lifespan: family-living	0.02	0.03	NO: 0.00 YES: -0.10	na (-5.17, -1.96)
nest predation risk: helper presence	0.01	0.01	NO: 0.00 YES: -0.01	na (-3.41, 0.27)

*: sum of model weights from Table S15 including the focal predictor. na – not applicable.

†: predictor weight relative to the highest weighted predictor.

‡: model averaging estimates according to full model averaging approach since the best AIC_c model is not strongly weighted (weight = 0.05) (Symonds and Moussalli 2011).

§: reference levels of categorical variables have an estimate of 0; estimates reflect difference in slope between the reference level and focal level.

Note: The relative importance of body mass and sex is due to their inclusion by default in each model to control for allometry and sex differences. All continuous variables are centered and scaled.

¶: predictors reflecting the relationship between LRS and AFR, see Table 1 and the Indices and estimates section of Materials and methods.

Table S14. Model with 90CI indices (see Table 4 for comparison). Relative importance of predictors included in the full model for the analysis of Delay Index variation including Lifespan Effect Index (N = 22 populations, 21 species) and model averaging estimates (based on 45 models with Δ AICc ($AICc_{focal\ model}$ – $AICc_{best\ model}$) ≤ 5, see Table S16).

Predictors	Predictor weight*	Relative importance of predictors†	Model averaging estimates‡,§	95% CI
intercept			0.64	(-0.24, 1.52)
ln(body mass)	0.61	1.00	0.47	(-0.02, 0.96)
sex	0.61	1.00	Both: 0.00 Female: -0.82 Male: -0.59	na (-1.51, 0.34) (-1.52, 0.34)
Lifespan Effect Index ¶	0.61	1.00	0.47	(0.25, 0.69)
Choice Index 90CI ¶	0.58	0.96	0.34	(0.11, 0.61)
Before Variation Index 90CI ¶	0.32	0.52	0.12	(-0.09, 0.56)
Before Variation Index 90CI: Choice Index 90CI	0.31	0.51	0.25	(0.18, 0.83)
After Variation Index 90CI ¶	0.29	0.47	-0.12	(-0.51, -0.01)
family-living	0.16	0.27	NO: 0.00 YES: -0.25	na (-2.30, 0.45)
nest predation risk	0.15	0.25	0.10	(-0.01, 0.82)
helper presence	0.15	0.25	NO: 0.00 YES: 0.42	na (-1.19, 4.58)
chick development mode	0.09	0.15	Altricial: 0.00 Precocial: -0.08	na (-1.27, 0.18)
mean lifespan	0.08	0.14	-0.02	(-0.94, 0.71)
latitude	0.08	0.14	0.03	(-0.33, 0.70)
Mean lifespan: helper presence	0.04	0.06	NO: 0.00 YES: 0.20	na (-0.44, 7.34)
Choice Index: helper presence	0.01	0.02	NO: 0.00 YES: -0.03	na (-2.45, -0.28)
Choice Index: family-living	0.01	0.02	NO: 0.00 YES: 0.01	na (-0.11, 0.80)

*: sum of model weights from Table S16 including the focal predictor. na – not applicable.

†: predictor weight relative to the highest weighted predictor.

‡: model averaging estimates according to full model averaging approach since the best AIC_c model is not strongly weighted (weight = 0.06) (Symonds and Moussalli 2011).

§: reference levels of categorical variables have an estimate of 0; estimates reflect difference in slope between the reference level and focal level.

Note: The relative importance of body mass and sex is due to their inclusion by default in each model to control for allometry and sex differences. All continuous variables are centered and scaled.

¶: predictors reflecting the relationship between LRS or survival and AFR, see Table 1 and the Indices and estimates section of Materials and methods.

Table S15. Model with 90CI indices (see Table S9 for comparison). Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index (following on the next page).

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS with AFR			Interactions									Model information				
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index 90CI	Before Variation Index 90CI	After Variation Index 90CI	After Variation Index 90CI : Before Variation Index 90CI	After Variation Index 90CI : Choice Index 90CI	Before Variation Index 90CI : Choice Index 90CI	Choice Index 90CI : helper presence	Choice Index 90CI : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.27	0.16	+	-	0.44	-	-	-	-	0.52	0.31	-0.25	-	-	0.81	-	-	-	-	-	-	11	-67.68	162.63	0.00	0.04
0.32	0.13	+	-	0.49	-	-	-	-	0.59	0.56	-0.25	-0.14	-	1.03	-	-	-	-	-	-	12	-66.22	162.80	0.17	0.04
0.22	0.25	+	-	0.35	-	-	-	-	0.47	0.23	-	-	-	0.71	-	-	-	-	-	-	10	-69.72	163.76	1.12	0.02
0.57	0.29	+	-	0.62	-	-	-0.33	-	0.61	0.60	-0.23	-0.17	-	1.11	-	-	-	-	-	-	13	-65.15	163.89	1.26	0.02
0.63	0.29	+	-	-	-	-	-	+	0.49	0.19	-	-	-	0.76	-	-	-	-	-	-	10	-69.83	163.98	1.34	0.02
0.47	0.18	+	-	0.27	-	-	-	+	0.51	0.21	-	-	-	0.80	-	-	-	-	-	-	11	-68.66	164.61	1.97	0.02
0.44	0.27	+	-	0.53	-	-	-0.23	-	0.52	0.30	-0.24	-	-	0.83	-	-	-	-	-	-	12	-67.19	164.74	2.11	0.02
0.50	0.09	+	-	0.36	+	-	-	-	0.55	0.29	-0.27	-	-	0.88	-	-	-	-	-	+	13	-65.61	164.81	2.17	0.01
0.42	0.12	+	-	0.37	-	-	-	+	0.53	0.29	-0.22	-	-	0.85	-	-	-	-	-	-	12	-67.26	164.88	2.24	0.01
0.48	0.09	+	-	0.41	-	-	-	+	0.61	0.54	-0.21	-0.15	-	1.09	-	-	-	-	-	-	13	-65.68	164.94	2.30	0.01
0.35	0.45	+	-	-	-	-	-	-	0.43	0.22	-	-	-	0.62	-	-	-	-	-	-	9	-71.77	165.01	2.37	0.01
0.46	0.17	+	0.11	0.48	-	-	-	-	0.53	0.31	-0.25	-	-	0.83	-	-	-	-	-	-	12	-67.46	165.29	2.65	0.01
0.43	0.38	+	-	0.46	-	-	-0.28	-	0.48	0.23	-	-	-	0.75	-	-	-	-	-	-	11	-69.01	165.29	2.66	0.01
0.29	0.14	+	-	0.45	+	-	-	-	0.53	0.32	-0.26	-	-	0.82	-	-	-	-	-	-	12	-67.49	165.34	2.71	0.01
0.53	0.07	+	-	0.41	+	-	-	-	0.61	0.53	-0.27	-0.14	-	1.09	-	-	-	-	-	+	14	-64.27	165.47	2.84	0.01
0.51	0.14	+	0.11	0.52	-	-	-	-	0.60	0.56	-0.25	-0.15	-	1.05	-	-	-	-	-	-	13	-65.97	165.52	2.89	0.01
0.29	0.15	+	-	0.44	-	+	-	-	0.52	0.31	-0.25	-	-	0.81	-	-	-	-	-	-	12	-67.60	165.56	2.93	0.01
0.34	0.11	+	-	0.50	+	-	-	-	0.60	0.57	-0.26	-0.14	-	1.05	-	-	-	-	-	-	13	-66.02	165.63	3.00	0.01
0.39	0.17	+	-	0.34	+	+	-	-	0.49	0.29	-0.26	-	-	0.77	+	+	-	-	-	-	15	-62.63	165.69	3.06	0.01
0.27	0.15	+	-	0.45	-	-	-	-	0.53	0.32	-0.25	-	-0.03	0.81	-	-	-	-	-	-	12	-67.67	165.71	3.07	0.01
0.33	0.12	+	-	0.49	-	+	-	-	0.59	0.56	-0.25	-0.14	-	1.04	-	-	-	-	-	-	13	-66.13	165.84	3.20	0.01
0.64	0.28	+	-	-	-	-	-	+	0.50	0.24	-0.13	-	-	0.78	-	-	-	-	-	-	11	-69.29	165.86	3.22	0.01

Table S15 following. Model with 90CI indices (see Table S9 for comparison). Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index.

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS with AFR			Interactions									Model information				
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index 90CI	Before Variation Index 90CI	After Variation Index 90CI	After Variation Index 90CI : Before Variation Index 90CI	After Variation Index 90CI : Choice Index 90CI	Before Variation Index 90CI : Choice Index 90CI	Choice Index 90CI : helper presence	Choice Index 90CI : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.41	0.42	+	-	-	-	-	-	-	0.45	0.27	-0.17	-	-	0.67	-	-	-	-	-	-	10	-70.84	166.00	3.36	0.01
0.32	0.13	+	-	0.49	-	-	-	-	0.59	0.56	-0.25	-0.14	-0.02	1.03	-	-	-	-	-	-	13	-66.22	166.01	3.38	0.01
0.37	0.45	+	-	-	+	+	-	-	0.39	0.19	-	-	-	0.57	+	+	-	-	-	-	13	-66.27	166.13	3.49	0.01
0.43	0.27	+	0.11	0.39	-	-	-	-	0.48	0.23	-	-	-	0.73	-	-	-	-	-	-	11	-69.48	166.24	3.61	0.01
0.43	0.14	+	-	0.38	+	+	-	-	0.56	0.53	-0.26	-0.14	-	0.99	+	+	-	-	-	-	16	-61.11	166.31	3.67	0.01
0.28	0.14	+	-	0.17	+	+	0.12	-	0.38	0.31	-0.28	-	-	0.55	-	-	+	+	-	+	17	-59.22	166.34	3.71	0.01
0.44	0.20	+	-	0.27	+	-	-	-	0.50	0.21	-	-	-	0.77	-	-	-	-	-	+	12	-68.02	166.41	3.78	0.01
0.45	0.24	+	-0.11	-	-	-	-	+	0.49	0.20	-	-	-	0.77	-	-	-	-	-	-	11	-69.59	166.47	3.83	0.01
0.24	0.25	+	-	0.35	-	+	-	-	0.47	0.23	-	-	-	0.71	-	-	-	-	-	-	11	-69.66	166.60	3.97	0.01
0.23	0.24	+	-	0.36	+	-	-	-	0.48	0.23	-	-	-	0.72	-	-	-	-	-	-	11	-69.67	166.62	3.98	0.01
0.66	0.24	+	-	0.55	-	-	-0.29	+	0.62	0.58	-0.20	-0.17	-	1.15	-	-	-	-	-	-	14	-64.87	166.68	4.04	0.01
0.42	0.04	+	-	0.47	+	+	-	-	0.56	0.32	-0.29	-	-	0.87	-	-	-	-	-	-	13	-66.60	166.78	4.15	0.01
0.71	0.27	+	-	-	-	-	-	+	0.56	0.45	-0.12	-0.12	-	0.98	-	-	-	-	-	-	12	-68.25	166.88	4.24	0.01
0.45	0.40	+	-	-	+	+	-	-	0.41	0.24	-0.19	-	-	0.62	+	+	-	-	-	-	14	-64.97	166.88	4.25	0.01
0.64	0.29	+	-	-	-	+	-	+	0.49	0.19	-	-	-	0.76	-	-	-	-	-	-	11	-69.80	166.89	4.25	0.01
0.62	0.28	+	-	-	-	-	0.02	+	0.49	0.19	-	-	-	0.76	-	-	-	-	-	-	11	-69.83	166.94	4.30	0.01
0.63	0.29	+	-	-	+	-	-	+	0.49	0.19	-	-	-	0.76	-	-	-	-	-	-	11	-69.83	166.94	4.31	0.01
0.58	0.28	+	-	0.36	-	-	-0.20	+	0.51	0.21	-	-	-	0.81	-	-	-	-	-	-	12	-68.29	166.96	4.32	0.01
0.30	0.29	+	-	0.24	+	+	-	-	0.43	0.21	-	-	-	0.65	+	+	-	-	-	-	14	-65.01	166.96	4.33	0.01
0.46	0.01	+	-	0.51	+	+	-	-	0.63	0.57	-0.29	-0.15	-	1.10	-	-	-	-	-	-	14	-65.08	167.09	4.45	0.00
0.58	0.28	+	-	0.62	-	+	-0.33	-	0.61	0.60	-0.23	-0.17	-	1.11	-	-	-	-	-	-	14	-65.10	167.14	4.50	0.00
0.56	0.27	+	-	0.62	+	-	-0.32	-	0.61	0.60	-0.23	-0.17	-	1.11	-	-	-	-	-	-	14	-65.13	167.19	4.55	0.00

Table S15 following. Model with 90CI indices (see Table S9 for comparison). Model selection output for the analysis of Delay Index variation excluding Lifespan Effect Index.

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS with AFR			Interactions									Model information				
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index 90CI	Before Variation Index 90CI	After Variation Index 90CI	After Variation Index 90CI : Before Variation Index 90CI	After Variation Index 90CI : Choice Index 90CI	Before Variation Index 90CI : Choice Index 90CI	Choice Index 90CI : helper presence	Choice Index 90CI : family-living	mean lifespan : helper presence	mean lifespan : family-living	nest predation risk : helper presence	nest predation risk : family-living	df	log Lik	AICc	Δ AICc	weight
0.55	0.29	+	-0.01	0.62	-	-	-0.34	-	0.61	0.60	-0.23	-0.18	-	1.11	-	-	-	-	-	-	14	-65.15	167.24	4.60	0.00
0.57	0.29	+	-	0.62	-	-	-0.33	-	0.61	0.60	-0.23	-0.17	-0.01	1.11	-	-	-	-	-	-	14	-65.15	167.24	4.61	0.00
0.54	0.37	+	-	-	+	+	-	+	0.43	0.17	-	-	-	0.68	+	+	-	-	-	-	14	-65.21	167.35	4.72	0.00
0.53	0.22	+	-	0.46	-	-	-0.19	+	0.53	0.29	-0.21	-	-	0.86	-	-	-	-	-	-	13	-66.93	167.44	4.81	0.00
0.26	0.09	+	-	0.16	+	+	0.17	-	0.38	0.31	-0.29	-	-	0.53	-	-	+	+	+	+	18	-57.77	167.45	4.82	0.00
0.45	0.41	+	-	-	-	-	-	-	0.50	0.45	-0.16	-0.11	-	0.83	-	-	-	-	-	-	11	-70.11	167.49	4.86	0.00
0.27	0.14	+	-	0.16	+	+	0.14	-	0.39	0.30	-0.26	-	-	0.52	+	-	+	+	-	+	18	-57.81	167.53	4.89	0.00

Model set with Δ AICc ≤ 5. N = 36 populations, 34 species.

"+" and "-" indicate the presence or absence of the parameter in the model, respectively. "df" is the degree of freedom. "log Likelihood" is the log likelihood of the model. "AIC_c" represents the Akaike's information criterion corrected for sample size. "Δ AIC_c" is the difference in AIC_c between the focal model and the model with the lowest AIC_c. "weight" represents the relative probability of a model within the full set of models.

Table S16. Model with 90CI indices (see Table S10 for comparison). Model selection output for the analysis of Delay Index variation including Lifespan Effect Index (following on the next page).

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS or survival with AFR				Interactions						Model information				
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index 90CI	Before Variation Index 90CI	After Variation Index 90CI	Lifespan Effect Index	Before Variation Index 90CI : Choice Index 90CI	Choice Index 90CI : helper presence	Choice Index 90CI : family-living	mean lifespan: helper presence	mean lifespan: family-living	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.59	0.22	+	-	0.42	-	-	-	-	0.47	0.32	-0.26	0.44	0.58	-	-	-	-	-	12	-24.05	85.66	0.00	0.06
0.82	0.53	+	-	-	-	-	-	-	0.42	0.17	-	0.40	0.47	-	-	-	-	-	10	-28.54	85.89	0.23	0.05
0.88	0.51	+	-	-	-	-	-	-	0.42	0.17	-0.21	0.41	0.48	-	-	-	-	-	11	-26.67	86.34	0.69	0.04
0.57	0.30	+	-	0.34	-	-	-	-	0.46	0.28	-	0.42	0.54	-	-	-	-	-	11	-27.01	87.02	1.37	0.03
0.51	0.48	+	-	-	-	-	-	-	0.30	-	-	0.55	-	-	-	-	-	-	8	-32.89	87.10	1.45	0.03
0.55	0.50	+	-	-	-	-	-	+	0.30	-	-0.31	0.53	-	-	-	-	-	-	10	-29.21	87.22	1.56	0.03
0.32	0.14	+	-	0.56	-	-	-	+	0.43	0.39	-0.37	0.46	0.47	-	-	-	-	-	13	-22.53	87.60	1.95	0.02
0.45	0.52	+	-	-	+	+	-	-	0.26	-	-	0.50	-	-	-	-	-	-	10	-29.40	87.61	1.95	0.02
0.80	0.76	+	0.29	-	+	+	-	-	0.23	-	-	0.51	-	-	-	-	-	-	11	-27.58	88.15	2.50	0.02
0.57	0.46	+	-	-	-	-	-	-	0.30	-	-0.20	0.56	-	-	-	-	-	-	9	-31.62	88.17	2.52	0.02
0.49	0.48	+	-	-	+	-	-	-	0.26	-	-	0.56	-	-	-	-	-	-	9	-31.64	88.21	2.55	0.02
1.00	0.95	+	0.42	-	+	+	-0.18	-	-	-	-	0.49	-	-	-	+	-	-	12	-25.36	88.29	2.63	0.02
0.50	0.50	+	-	-	+	+	-	-	0.26	-	-0.21	0.51	-	-	-	-	-	-	11	-27.75	88.50	2.84	0.01
0.39	0.13	+	-	-	-	-	0.36	-	0.28	-	-0.28	0.52	-	-	-	-	-	-	10	-29.97	88.74	3.08	0.01
0.68	0.99	+	-	-	+	+	-0.49	-	0.24	-	-	0.52	-	-	-	-	-	-	11	-27.95	88.90	3.25	0.01
0.49	0.51	+	-	-	-	-	-	+	0.30	-	-	0.53	-	-	-	-	-	-	9	-32.08	89.09	3.43	0.01
0.82	0.55	+	-	-	-	+	-	-	0.44	0.16	-	0.38	0.47	-	-	-	-	-	11	-28.06	89.12	3.46	0.01
0.55	0.46	+	-	-	+	-	-	-	0.26	-	-0.21	0.57	-	-	-	-	-	-	10	-30.17	89.14	3.49	0.01
0.40	0.34	+	-	0.24	-	-	-	+	0.32	-	-0.34	0.57	-	-	-	-	-	-	11	-28.28	89.56	3.90	0.01
0.40	0.30	+	-	-	-	-	0.20	-	0.29	-	-	0.53	-	-	-	-	-	-	9	-32.34	89.60	3.95	0.01
0.77	0.52	+	-	-	+	-	-	-	0.39	0.18	-	0.41	0.43	-	-	-	-	-	11	-28.33	89.65	4.00	0.01
0.79	0.52	+	-	-	-	-	-	+	0.40	0.19	-0.27	0.41	0.40	-	-	-	-	-	12	-26.07	89.70	4.04	0.01
0.59	0.24	+	-	0.41	-	+	-	-	0.48	0.31	-0.25	0.41	0.58	-	-	-	-	-	13	-23.60	89.74	4.08	0.01
1.01	1.07	+	0.37	-	+	+	-0.29	-	0.14	-	-	0.50	-	+	-	+	-	-	14	-20.90	89.80	4.14	0.01
0.46	0.46	+	-	-	+	-	-	-	0.20	-	-	0.52	-	-	+	-	-	-	10	-30.51	89.82	4.16	0.01

Table S16 following. Model with 90CI indices (see Table S10 for comparison). Model selection output for the analysis of Delay Index variation including Lifespan Effect Index.

	Covariate		Ecological factors		Social lifestyle factors		Life-history factors		Indices reflecting change in LRS or survival with AFR				Interactions						Model information				
(Intercept)	ln(body mass)	sex	latitude	nest predation risk	family-living	helper presence	mean lifespan	chick development mode	Choice Index 90CI	Before Variation Index 90CI	After Variation Index 90CI	Lifespan Effect Index	Before Variation Index 90CI : Choice Index 90CI	Choice Index 90CI : helper presence	Choice Index 90CI : family-living	mean lifespan: helper presence	mean lifespan: family-living	nest predation risk : family-living	df	log Likelihood	AICc	Δ AICc	weight
0.38	0.41	+	-0.10	-	-	-	-	-	0.30	-	-	0.53	-	-	-	-	-	-	9	-32.46	89.84	4.19	0.01
0.71	0.43	+	-0.10	-	-	-	-	-	0.41	0.20	-0.24	0.39	0.46	-	-	-	-	-	12	-26.15	89.86	4.20	0.01
0.72	0.31	+	-	-	-	-	0.20	-	0.40	0.19	-0.26	0.40	0.43	-	-	-	-	-	12	-26.15	89.86	4.20	0.01
0.74	0.49	+	-0.05	-	-	-	-	-	0.42	0.18	-	0.40	0.46	-	-	-	-	-	11	-28.44	89.87	4.22	0.01
0.88	0.53	+	-	-	-	+	-	-	0.43	0.17	-0.21	0.39	0.48	-	-	-	-	-	12	-26.19	89.94	4.28	0.01
0.40	0.37	+	-	0.17	-	-	-	-	0.31	-	-	0.58	-	-	-	-	-	-	9	-32.52	89.96	4.31	0.01
0.80	0.50	+	-	-	-	-	0.03	-	0.42	0.17	-	0.40	0.46	-	-	-	-	-	11	-28.53	90.06	4.41	0.01
0.82	0.53	+	-	-	-	-	-	+	0.42	0.17	-	0.40	0.46	-	-	-	-	-	11	-28.54	90.08	4.43	0.01
0.38	0.36	+	-0.14	-	-	-	-	-	0.29	-	-0.24	0.54	-	-	-	-	-	-	10	-30.66	90.12	4.46	0.01
0.51	0.50	+	-	-	-	+	-	-	0.31	-	-	0.53	-	-	-	-	-	-	9	-32.62	90.16	4.51	0.01
0.71	1.09	+	-	-	+	+	-0.61	-	0.20	-	-	0.50	-	+	-	+	-	-	13	-23.81	90.17	4.51	0.01
0.64	0.97	+	-	-	+	+	-0.58	-	-	-	-	0.48	-	-	-	+	-	-	11	-28.64	90.28	4.62	0.01
0.86	0.79	+	0.35	-	+	+	-	-	0.16	-	-	0.50	-	-	+	-	-	-	12	-26.36	90.28	4.63	0.01
0.83	0.50	+	-	-	+	-	-	-	0.39	0.18	-0.22	0.42	0.44	-	-	-	-	-	12	-26.38	90.33	4.67	0.01
0.52	0.19	+	-0.05	0.40	-	-	-	-	0.46	0.32	-0.27	0.43	0.56	-	-	-	-	-	13	-23.91	90.37	4.72	0.01
0.57	0.49	+	-	-	-	-	-	-	0.30	-0.06	-	0.56	-	-	-	-	-	-	9	-32.75	90.42	4.76	0.01
0.84	0.74	+	0.37	-	+	+	-	-	-	-	-	0.48	-	-	-	-	-	-	10	-30.87	90.53	4.88	0.01
0.60	0.23	+	-	0.43	-	-	-0.02	-	0.47	0.32	-0.25	0.44	0.58	-	-	-	-	-	13	-24.04	90.62	4.97	0.01
0.59	0.22	+	-	0.42	+	-	-	-	0.47	0.32	-0.26	0.44	0.57	-	-	-	-	-	13	-24.04	90.64	4.98	0.00
0.54	0.52	+	-	-	-	+	-	+	0.31	-	-0.31	0.51	-	-	-	-	-	-	11	-28.83	90.65	5.00	0.00

Model set with Δ AICc ≤ 5. N = 22 populations, 21 species.

"+" and "-" indicate the presence or absence of the parameter in the model, respectively. "df" is the degree of freedom. "log Likelihood" is the log likelihood of the model. "AIC_c" represents the Akaike's information criterion corrected for sample size. "Δ AIC_c" is the difference in AIC_c between the focal model and the model with the lowest AIC_c. "weight" represents the relative probability of a model within the full set of models.

Figure S1. Phylogenetic tree for the 34 species studied in this paper (based on the full tree from Jetz et al. 2012; Ericson backbone phylogeny).

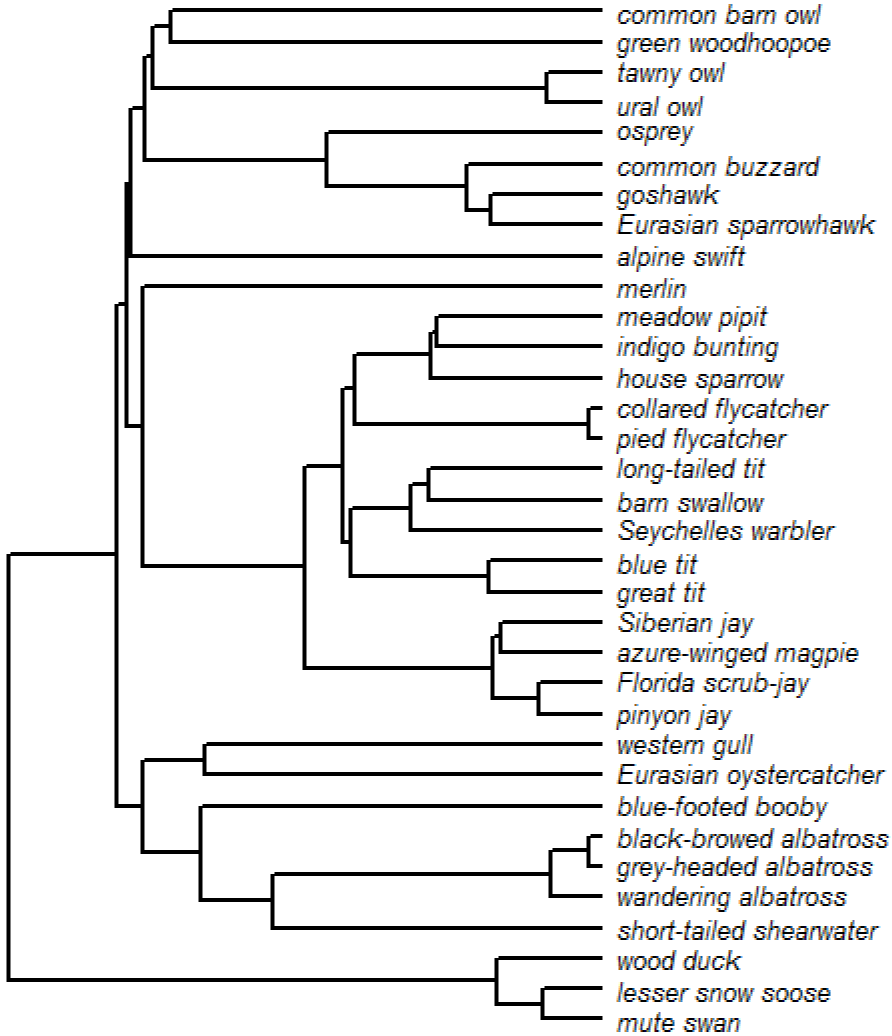


Figure S2. Variation in AFR and consequences for mean reproductive lifespan. Relationship between mean reproductive lifespan (mean lifespan (per AFR classes) minus AFR) and AFR for 22 populations (21 species) used to estimate the Lifespan Effect Index (Table 1); each point represents the mean value for individuals that start to reproduce at a specific AFR. B = both sexes, F = female, M = male.

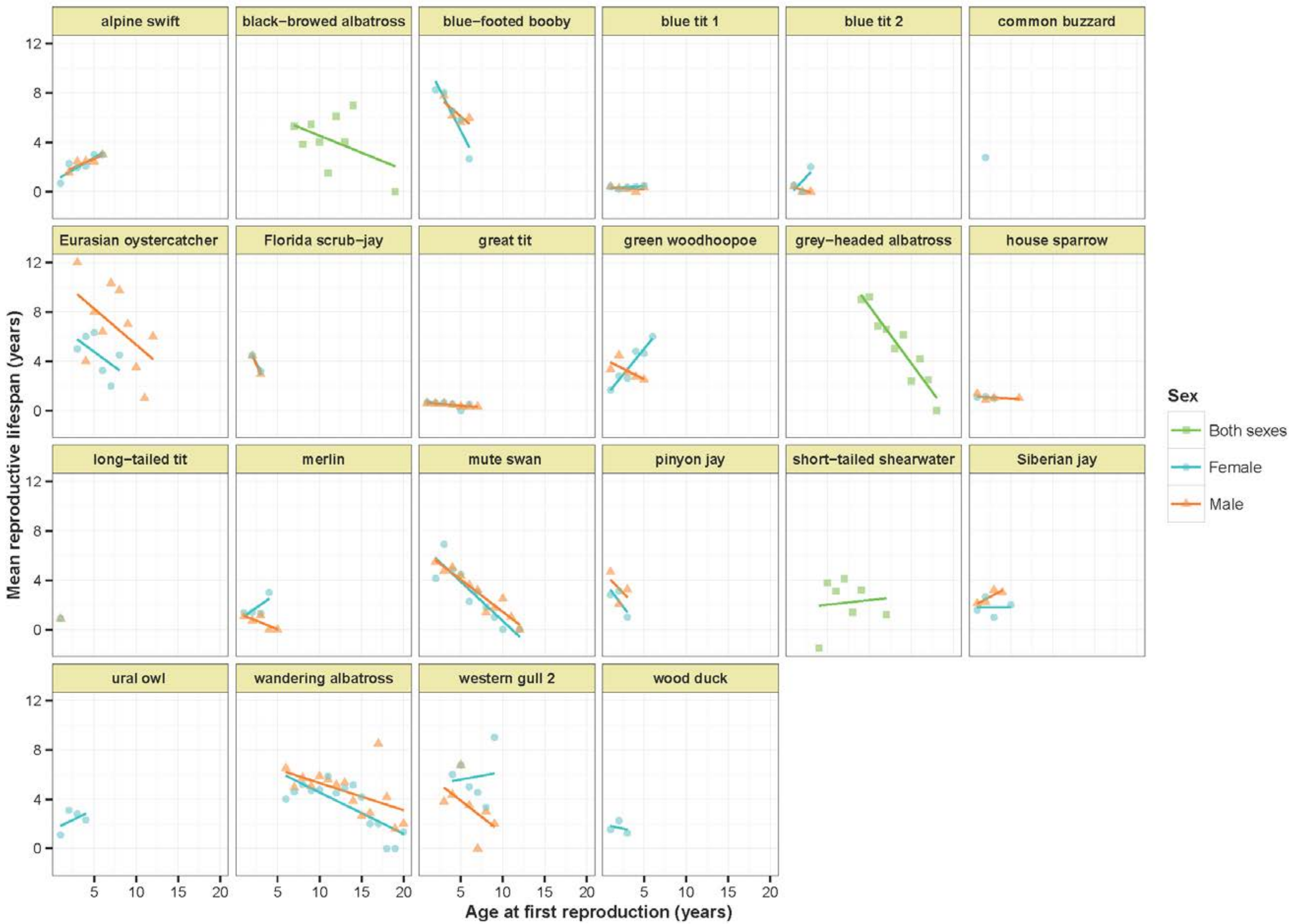
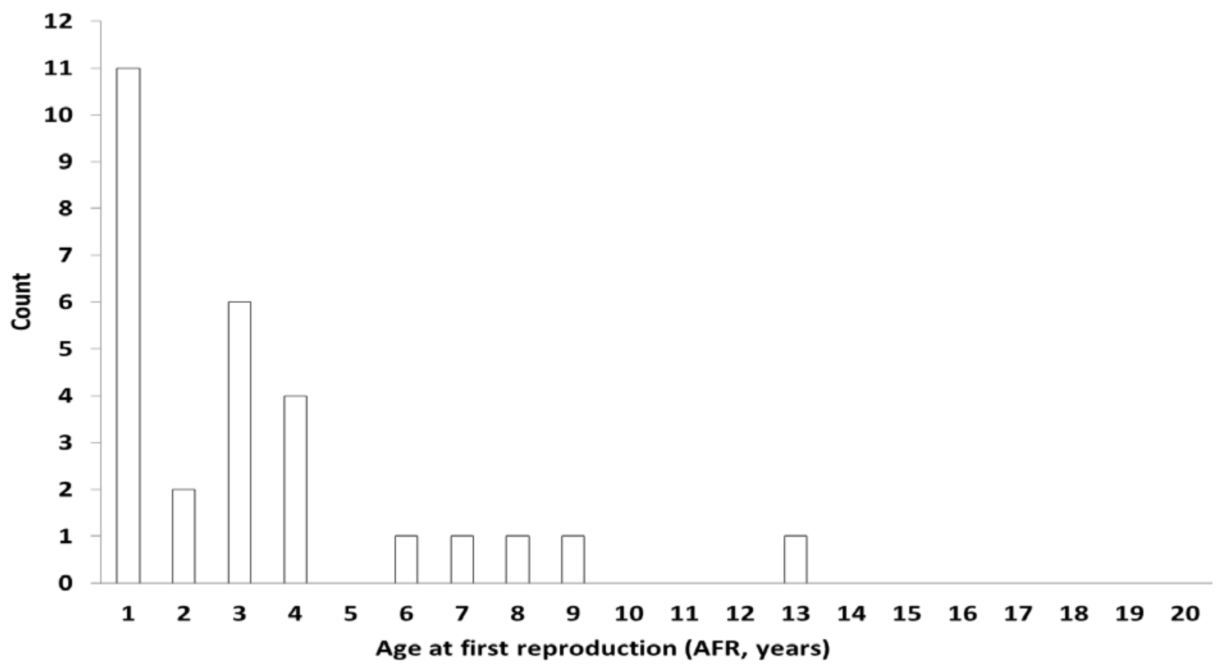


Figure S3. Variation in AFR. (**A**) Number of times the specific AFR corresponded to a species modal AFR (over 28 out of 34 species as we excluded 4 species with only 1 AFR age class and 2 species for which the sample size per AFR age class was missing). (**B**) Frequency of observation of a specific AFR age class across all 34 species (an AFR age-class was counted as being observed within a population when at least one individual initiated reproduction at the focal AFR – e.g. a values of about 20% for an AFR of 9 means that about 7 species (20% of 34) had individuals that initiated their reproduction at age 9).

A



B

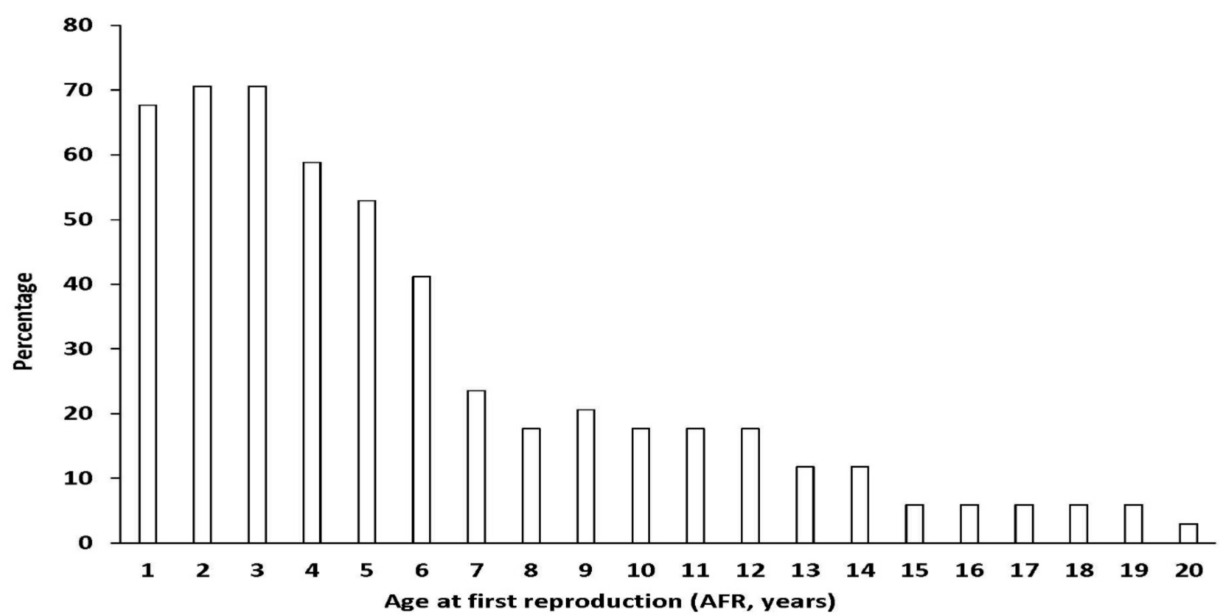
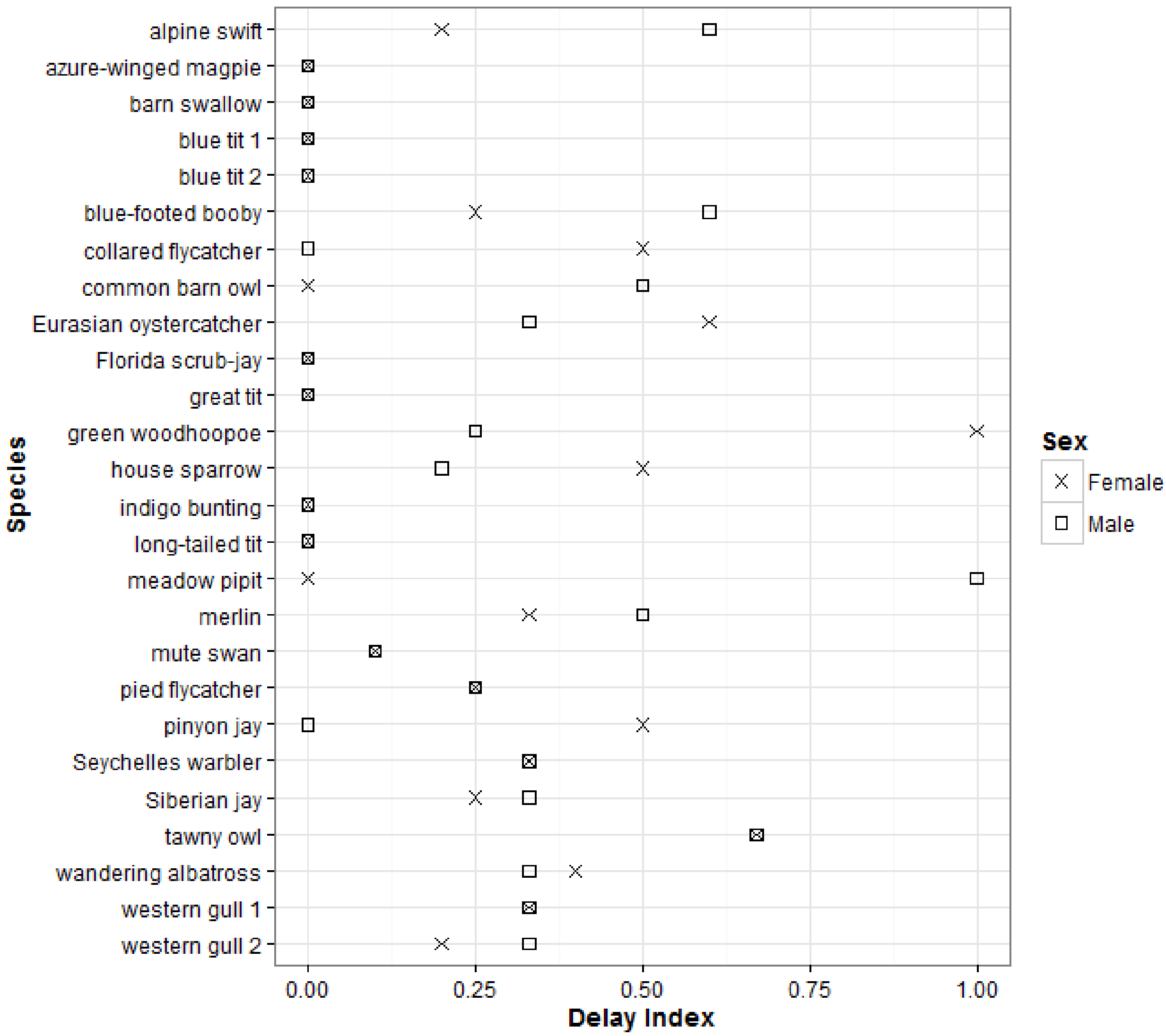


Figure S4. Sex differences in the Delay Index for the 26 populations (24 species) for which we had separate data for males (M, square symbols) and females (F, cross symbols). A number after the species indicates separate studies.



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